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FRED J. HOLL

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SEASONAL MIGRATION OF MULE DEER

By

CARL PARCHER RUSSELL

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SEASONAL MIGRATION OF MULE DEER

INTRODUCTION

True seasonal migrations of animals bring about changes of range. They periodically recur and alternate in direction. Such movements are known among crustaceans, fishes, reptiles, birds, and mammals (Cahn, 1925; Coward, 1912; Meek, 1916). Long before the Christian Era, the problem of bird migration was a subject of speculation among philosophers, and through the ages the matter has found place in the literature of many lands (Wetmore, 1926). Today, after many workers have given attention to the problem, it is yet impossible to be sure which causative factors are responsible for the remarkable seasonal movements of birds (Wetmore, 1926).

The migratory habits of the mule deer, *Odocoileus hemionus*, have been noted in the writings of explorers and naturalists since the first noteworthy reference to the species by Lewis and Clark in 1814 (Thwaites, 1904). The first printed mention of the species was that of Edward Umfreville, 1789. Migration, however, has been accepted as a commonplace habit by which the mule deer, like other migratory species, gains certain advantageous ends, and, to the best of the writer's knowledge, no attempt has been made to inquire into the causative factors in the seasonal movements, nor has the biological significance of the migration ever received consideration. The question as to *why* a species habitually migrates constitutes a problem in ecology that challenges any one who inquires into the philosophical aspects of field natural history, and in the present study it would appear that the problem is subject to attack by practical methods which are productive of concrete results.

Twice each year the herds of mule deer of the mountains of the western United States change their range. Their winter habitat comprises favored valleys and slopes three thousand to six thousand feet above sea level. In the spring, the greater number of the animals leave their winter homes and climb to higher valleys and plateaus. This movement may involve a climb of five or six thousand feet and travel over a horizontal distance of fifty miles. Seton (1927) calls attention to a Colorado locality where the drift involves travel over a 150 mile route. In the fall, the movement is reversed. The area occupied in winter is referred to as the *winter range*, and the territory in which the summer is spent as the *summer range*. Lanes of travel between the two are *migration routes*. The migration itself is commonly referred to as the *drift*.

It is the purpose of this paper to point out the details of mule deer migrations, to describe the correlation of these movements with other phases of the animal's life history and with periodic physical phenomena, and to demonstrate that definite facts are available which are subject to interpretation.

METHODS OF STUDY

In 1923, the writer assumed the duties of park naturalist in Yosemite National Park. Exceptional opportunities for study of the life history of the mule deer of the region encouraged an immediate undertaking of field work. The study was pursued in connection with official duties and continued through a part of 1928. In the summer of 1928, the writer was transferred to Yellowstone National Park, Wyoming, and he took advantage of the opportunity to continue study of the mule deer in that region. The same general procedure was followed for another three years, and a careful comparison of habits and movements was made for the two regions, the central Sierra Nevada and the Yellowstone section of the Rocky Mountains. Residence in Yosemite National Park was continuous from June, 1923 to July, 1928. The Yellowstone studies were limited to seven months of each year, but they are representative of all seasons and adequate for comparison with the Yosemite findings.

Field work was not spasmodic but was carried on daily or at intervals of a day or two. Food plants were collected after deer were observed to partake of them, and the specimens were identified by the writer or submitted to specialists for identification. In Yellowstone, Dr. W. B. McDougal assisted. In Yosemite, the park botanist, Mrs. Enid Michael, aided in this work. The herbaria of the Yellowstone Museum and the Yosemite Museum were most helpful in the undertaking. Stomach contents were examined in the laboratories of the Yosemite Museum and the Yellowstone Museums. During the slaughter of the northern herd of Yosemite deer, because of the epidemic of foot and mouth disease, 1924-1925 (Mohler, 1926), many stomachs were given cursory examinations in the field.

All life zones and ecological situations received full consideration. In Yosemite, the entire park was given careful study, and outlying regions to a distance of thirty to fifty miles were included. The entire range of the Yosemite deer herds was under observation. Regions not penetrated by roads were visited with pack outfits. The Yosemite road system is good, and the use of an automobile greatly facilitated field work. In winter, the upper reaches of the park were inaccessible to automobiles, and trips were made on snowshoes or skis. In Yellowstone, all of the park was studied with the exception of the southeast corner. In this park, too, a comprehensive system of roads made possible the study of large areas at frequent intervals. Some regions inaccessible to automobiles were visited on foot or in the saddle.

ACKNOWLEDGMENTS

The extensive territory involved in the Yellowstone study necessitated wide coöperation from a small army of national park and national forest employees. It was possible to secure the cordial interest of the supervisors of

nine national forests, and it is to be acknowledged that without their assistance results here presented would necessarily have been limited to areas much smaller than those actually covered in this treatment.

The following U. S. Forest Service officials have assisted by making special studies and reports or by placing results of their routine game studies at my disposal: Supervisors Roy Boothe, Inyo National Forest, Bishop, California; W. W. Maule, Mono National Forest, Minden, Nevada; J. R. Hall, Stanislaus National Forest, Sonora, California; R. T. Ferguson, Beartooth National Forest, Billings, Montana; J. N. Langworthy, Shoshone National Forest, Cody, Wyoming; S. W. Stoddard, Targhee National Forest, St. Anthony, Idaho; Acting Supervisor F. T. Carroll, Madison National Forest, Sheridan, Montana; Ranger E. P. White, Gallatin National Forest, Eldridge, Montana; and Range Examiner Arthur Cramer, Absaroka National Forest, Livingston, Montana.

In the course of much of the Yosemite work, I received the aid of George M. Wright, Assistant Park Naturalist. George Shedd of the Yosemite Park and Curry Company coöperated generously in making observations at Glacier Point (7200 ft.). Since leaving Yosemite, I have had many occasions to call on the Yosemite Museum staff for assistance. The Yellowstone National Park organization has developed a plan of wild life studies, results of which lent material aid in the present investigations. I am especially indebted to Chief Ranger George Baggeley; William Rush, in charge of elk study, and Dorr G. Yeager, park naturalist, for personally supporting my activities and arranging for the coöperation of some fifty Yellowstone park rangers and ranger-naturalists in making observations and reporting upon them. O. J. Murie of the United States Biological Survey and Superintendent Sam Woodwring of the Grand Teton National Park have given information on the movements of deer south of Yellowstone Park. W. T. Lathrop, meteorologist of the Yellowstone Weather Bureau Office, has given important assistance in supplying climatological data that were not available from published records. Other offices of the Weather Bureau have given coöperation, and published reports of that Bureau have been of prime importance in establishing some of the facts here presented. Dr. Lee R. Dice, Museum of Zoölogy, University of Michigan, has given of his time and interest in assisting through helpful criticism and suggestions during the preparation of this paper.

ROCKY MOUNTAIN MULE DEER OF YELLOWSTONE PARK

Yellowstone National Park is located in northwestern Wyoming, encroaching slightly upon Montana and Idaho. It contains some 3500 square miles of mountainous country, which saddles the backbone of the continent. The park center is a broad volcanic plateau approximately eight thousand feet above sea level. Surrounding it are mountain ranges with culminating peaks rising to ten and eleven thousand feet. North of the elevated plateau, the valley of the

Yellowstone drops to a level of five thousand three hundred feet. To the south, the lowest altitudes within the park are slightly higher than six thousand feet. In spite of the fact that the altitudinal variation is not great, Bailey (1930) has determined that a range of climate exists which includes four life zones. These are the Arctic-Alpine, Hudsonian, Canadian, and Transition. With the exception of the Arctic-Alpine Zone, this study of mule deer movements is concerned with all of the belts. Regions adjacent to the national park are largely national forest lands. They figure in this account, as shown on the accompanying map, because many of the park deer occupy winter ranges outside of the park boundaries.

OUTLINE OF HISTORY

The mule deer of the region are sturdy representatives of the species so frequently mentioned in the journals of Lewis and Clark (Thwaites, 1904), who in 1805-1806 observed them during their epochal journey across the northern end of the area with which this paper is concerned. The account of this exploration was not put in print until 1814. Charles Le Raye, an army man and adventurer of the early days of the Rocky Mountain fur trade, entered the Yellowstone region as a captive among Indian tribes in 1803. His journals (Cutler, 1812) provided the notes on mule deer which C. S. Rafinesque (1817) used as the basis for his description of the species. The type locality was "the Sioux River" (South Dakota).

Say (James, 1823) described a deer from "Major Long's Creek" (New Mexico) as *Cariacus macrotis*, and Caton (1876) used *Cervus macrotis californicus* as the name for a deer from "near Gaviota Pass, forty miles from Santa Barbara" (California). Merriam (1898) showed that *Odocoileus hemionus* was the specific name applicable for all of these deer. Bailey (1930) identifies the Yellowstone Park deer as *Odocoileus hemionus macrotis*, and Grinnell and Storer (1924) use *Odocoileus hemionus hemionus* for the Yosemite animal. No recent revision of the deer of this group has been made. It is probable that study will reveal subspecific differences not recognized at present, and for the purposes of this paper the name *Odocoileus hemionus* will therefore be used for Yellowstone and Yosemite animals alike.

SUMMER RANGE AND SUMMER ACTIVITIES

The 1930 game census taken by the ranger department of Yellowstone Park indicates a population of some 800 deer (Baggley, 1930). Most of these animals spend the summer on the central plateau. I have found no evidence that they travel higher than the 9000 foot level. Except for warm southwest exposures, timberline (upper edge of Hudsonian Zone) exists at about 9000 feet, and it is unlikely that deer often go above this belt. During the summer, deer are nowhere encountered in large herds. Two or three does with a spike buck, perhaps, may associate, but it is more common to find does

alone or with fawns of the year. Old bucks are usually alone but sometimes are accompanied by a younger male. Bucks are not frequently seen near the lanes of automobile travel but can be jumped from cover by searching higher slopes some few miles from roads, where favorable vegetation abounds.

REARING OF YOUNG

The Yellowstone deer arrive on summer range as soon as food plants have reached a stage of development attractive to them. This development of vegetation varies with the season and may result in the deer ascending to summer range between the middle of May and the first of July. The gray coat of winter gives way to the summer "red" early in June. Ordinarily, the young are born late in June or early in July, after the females have reached their favorite summer grounds. During this time, the does and bucks do not associate. The males tend to frequent levels slightly higher than the summer range of the does, and, as might be expected, the daily movements of the bucks take them over a wider range of territory than is covered by individual females. Hall (1927) has concluded that home range in summer covers an area of two square miles. My observations lead me to agree that bucks cover such a territory and that does with fawns are content with half that area. During many of the night and early morning hours, the animals are engaged in feeding. At midday and until late afternoon, they habitually recline in chosen spots, "beds," where they may chew cuds and relax. Usually, these resting places are selected with an eye for cover. They are often so situated that the approach of possible enemies may be from but one side, and that side is under constant surveillance by the reclining animal. It is not unusual for two or more animals to bed down near each other, in which case it is to be inferred that they divide their watchfulness in such a way as to command views of all avenues of approach to their bower. Caring for young, securing food from an abundance of forage plants, resting, and evading enemies make up the daily program of a mule deer on summer range.

FOOD HABITS

Most significant of summer activities from the standpoint of the problem with which this paper is chiefly concerned are the feeding habits. Deer are equipped with sharp lower incisors, which close upon the toothless tip of the upper jaw. Tough twigs and succulent herbs alike are cut by this mechanism. The biting off of forage involves a forward and upward movement of the head and allows close grazing or digging out of root systems, some of which are regularly sought by the animals. Buds, flowers, seeds, leaves, and twigs all come within the deer's bill of fare. The tongue is especially adapted for manipulating morsels of any variety, excluding from the mouth any unpalatable matter which inadvertently enters with food. However, the delicate nose and mouth of the deer permit of a precision of browsing and grazing

which makes for skillful selection of food. Feeding takes place rapidly, and there is but little chewing of vegetation before it enters the paunch. When this first stomach is filled, the deer retires to a place where it may recline in safety and there it chews its cud until the food is well masticated and passed on to the omasum and the true glandular stomach.

Food plants taken by deer on the Yellowstone summer range are of wide variety. Those listed have, for the most part, been observed by the writer to be actually fed upon. Rangers, ranger-naturalists, and Forest Service officials have added to the list. The list in its entirety would, perhaps, not be necessary for the purposes of this paper, but since little or nothing on food habits of Yellowstone deer has been made available, it seems desirable to present all results of the present study. Rydberg (1900) and Conard (1928) have been referred to for usage of names.

The following plants are commonly eaten by Yellowstone deer on their summer range: *Ceanothus velutinus*, redroot, "mountain mahogany"; *Chenopodium album*, pigweed; *Cornus instolonea*, red osier dogwood; Fungi—many species of mushrooms; *Lepargyrea canadensis*, Canadian buffalo-berry; *Polygonum amphibium*, false bistort, knot grass; *Populus tremuloides*, aspen; *Rubus strigosus*, red raspberry; *Salix pseudomonticola*, *S. pseudo-myrsinites*, and *S. wolfii idahoensis*, willows; *Sambucus melanocarpa*, elderberry; *Saxifraga saximontana*, saxifrage; *Sorbus scopulina*, mountain ash; *Taraxacum officinale*, dandelion; and *Trifolium rydbergii*, clover.

The following plants are apparently of intermediate importance: *Agropyron tenerum*, wheat grass; *Artemisia tridentata*, sage; *Aster adscendens*, *A. fremontii*, and *A. integrifolius*, asters; *Astragalus alpinus*, vetch; *Berberis repens*, Oregon grape; *Bromus porteri*, brome grass; *Calamagrostis canadensis*, grass; *Carex festivella*, *C. raynoldsii*, and *C. rostrata*, sedges; *Chamaenerion augustifolium*, fireweed; *Chrysothamnus lanceolatus*, rabbit brush; *Cogswellia platycarpa*, wild parsnip; *Delphinium glaucescens*, larkspur; *Festuca idahoensis*, fescue grass; *Fritillaria atropurpurea*, spotted lily; *Geranium viscosissimum*, red geranium; *Juncodes parviflorum*, woodrush; *Koeleria cristata*, June grass; *Lupinus parviflorus*, lupine; *Melica spectabilis*, melic grass; *Phleum alpinum*, timothy; *Poaepilis* and *P. pratensis*, blue grasses; *Potentilla fruticosa*, cinquefoil; *Ranunculus purshii* and *R. reptans*, buttercups; *Rhus trilobata*, sumac; *Ribes hudsonianum* and *R. parvulum*, currants; *Stipa richardsoni*, stipa grass; and *Vaccinium membranaceum*, low huckleberry.

It should be explained that this list is based on too few observations to be regarded as infallible. If a plant finds a place on the list because it was observed to be taken once, it has been grouped with others judged to be of "intermediate importance," yet further study might show that the same species is very commonly eaten, and perhaps more acceptable to the deer than some other species now listed as commonly eaten. The list is to be considered as

provisional. It finds its greatest value in that it provides a basis for comparison with winter food and offers a point of beginning for thorough investigation of the feeding habits of deer.

Summer food plants most frequently observed to be eaten are mountain mahogany (*Ceanothus velutinus*), pigweed (*Chenopodium album*), red osier dogwood (*Cornus instolonea*) mushrooms, Canadian buffalo-berry (*Lepargyrea canadensis*), aspen (*Populus tremuloides*), red raspberry (*Rubus strigosus*), willows of several species (*Salix*), elderberry (*Sambucus melanocarpa*), dandelion (*Taraxacum officinale*), and clover (*Trifolium*). During the early days of May, when deer first arrive on summer range, grasses (*Agropyron*, *Calamagrostis*, *Festuca*, *Koeleria*, *Melica*, *Poa*) are green and succulent and at this time take an important place on the animal's bill of fare. In fact, it seems to be the development of these grasses which controls the spring migration. Some few aspens, *Populus tremuloides*, not yet erect after the depressing effect of snow drifts, provide desirable browse in the form of new leaves. By the end of May, unless unusually cold weather prevails, other shrubs and forage plants (*Chenopodium*, *Lepargyrea*, *Rubus*, *Salix*, *Sambucus*, *Trifolium*) have produced an abundance of food, and normal life of the summer range is under way.

Deer on summer range are not greatly hampered by competition with other animals. Elk and moose frequent the same range, and the elk, especially, partake of many of the forage plants sought by the deer. The elk run in herds and noticeably affect the forage where they have browsed. I have noted that deer tend to avoid the areas occupied by elk in summer and that they do not feed in the immediate vicinity of regions over which elk have recently browsed. However, the deer of Yellowstone are comparatively few, and there is ample summer forage unaffected by elk.

Weights of stomach contents were recorded in three Yellowstone deer from summer range. None of the three was filled to capacity. The macerated food, a great percentage of which was not recognizable, weighed two pounds and one ounce in a male fawn about two months old, five pounds and four ounces in an adult doe, and five pounds and five ounces in a two year old buck.

FALL MIGRATION

In September, the central plateau region experiences temperatures well below freezing, and the vegetation assumes the aspect of fall. Willows and aspens turn yellow early in September, as do the plants of the open meadows. Not infrequently, snow storms occur in September. The snow of these early storms usually melts soon after falling, but at this time a restlessness develops in the deer of the upper limits (8500 feet) of summer range. Fall migration may be said to be initiated by these early storms, for a definite movement of deer from the highest levels takes place when they occur. This movement is

not the persistent descent to definite winter range which marks the true migration that later takes place from central summer range, but rather a deliberate extension of daily movements which results in travel to lower altitudes. The activity is not prompted by inaccessibility of food, for the first loose snow does not bury food plants to a depth of more than a few inches. It is, perhaps, a reaction to the warning provided by the fall in temperature, the presence of snow, and the changed condition of food. If snow storms do not occur until late October, when winter sets in earnestly and suddenly, there is a tendency for some of the deer to begin their descent in advance of snow storms. However, delayed winter conditions seem to delay fall migration.

DETAILS OF MOVEMENTS

By far the greater number of Yellowstone deer have spent the summer on ranges of intermediate altitudes (7500 feet). Here the does, fawns, and some bucks, especially the younger bucks, have congregated in small family groups, the daily movements of which have taken them over rather limited territory. In October, these have been joined, perhaps, by some of the old bucks that have spent the summer at higher levels and participated in the first "drift" of the fall. The first snow storms that affected the old bucks may also bring about some movement among the animals on the central summer range. A descent of a few of these animals often results in the appearance of deer at Mammoth and other parts of the winter range soon after the first storms of October. Animals at points distant, some fifty miles from their winter range, will at this time start a slow journey toward winter feeding grounds. This movement may not result in notable change in altitude, but it brings them within easy striking distance when the necessity for rapid descent is upon them. Such movements frequently just precede or coincide with the elk migration, and routes followed are usually parallel with the lanes of travel used by the elk. One interesting exception has been noted by Murie (1929, ms.), who finds that the deer of the Upper Yellowstone-Thorofare regions move eastward from the Yellowstone Valley, over the Absarokas to the Shoshone drainage system (Fig. 1). This is a marked departure from the usual establishment of migration routes, since a major divide between river systems is crossed. It would seem that habit forming must be responsible for the situation rather than simple environmental influences. The preliminary activity serves to stir the entire deer population, and, although by far the greater number of the animals are yet at levels more than a thousand feet above winter range, they are far from their home territory of the summer and in position to descend when forced to do so.

Severe storms usually occur in November. The restlessness, which for some weeks has been evident in the animals, culminates in a determined descent when the first severe storm arrives. The deer move in numbers to the true winter ranges and frequently seem to occupy their ancestral winter

homes overnight. If, after some days or weeks on winter range, mild weather conditions again prevail, there may be some ascent to regions immediately adjacent to, but a thousand feet above, winter range. Food plants at this altitude may differ markedly from the forage of adjacent valleys, yet they are utilized if snow conditions permit. No great distances are traveled during these untimely ascents, but the movements, nevertheless, constitute a desertion of what is ordinarily designated as winter range. With the return of severe winter conditions, the deer again move to lower levels. In other words, the deer of Yellowstone occupy that portion of their territory upon which food is available and adjacent to suitable winter range regardless of the calendar.

Coyotes and other predators prey upon the deer of Yellowstone Park (Skinner, 1927), but the extreme assertions of some of those concerned with control of predators in the park region (Henderson, 1930) (Cottrell, 1928) cannot be substantiated (Adams, 1930; Hall, 1930). Predators follow deer and other large mammals in migration, but I have found no evidence that they affect in any way the seasonal movements of deer.

INSTANCES OF ABSENCE OF MIGRATION

A significant instance of absence of migration is provided by the group of some seventy Yellowstone animals that regularly inhabit the Upper and Lower Geyser basins and the Firehole Valley between those basins and Madison Junction (Fig. 2). This area is 7500 feet above sea level, well within the summer range of the Central Plateau, and distinctly removed from other areas of winter range. No evidence of members of this group leaving their home territory has been noted by the park rangers who reside in the geyser basins throughout the year. These animals are assured of a ready food supply regardless of the severity of the winter. The heat of the geyser regions causes large tracts of land to be entirely free from snow, and the warm waters of brooklets and larger streams encourage the growth of mosses and grasses along their banks throughout the winter. These green plants provide a dependable food supply within certain limits, and it is unnecessary for the deer of the region to migrate.

WINTER RANGE AND WINTER ACTIVITIES

The area along the Gallatin, Lamar, Gardiner, and Yellowstone rivers constitutes the range to which the writer's study was given for the purposes of this paper. Other areas indicated on the accompanying map (Fig. 1) were under observation by National Park or Forest Service officials and were reported upon by them. During the period of heavy snow and low temperatures, the deer usually remain at altitudes below 7000 feet.

It is not unusual for the animals to congregate in herds in the regions in which resort is made to artificial feeding. Fifty-five is the maximum number I have observed in one herd at the game ranch below Gardiner. Park rangers

report herds of seventy as not unusual. Small bands of six to twelve are commonly encountered in all areas occupied as winter range. Late in the winter, bucks tend to separate from the bands of does and yearlings to forage alone or with one or two companions of their sex. In the region about the game ranch, they do not hesitate to join the herds of does and fawns about the hay at the time of feeding.

BREEDING

During the last weeks that the animals are on summer range, the fall molt takes place. Shedding may begin late in August and continue until the last of September. When the movement to winter range occurs, the animals are almost without exception in the full gray coat of winter. Antlers which have carried velvet all through the summer are polished, hard, and white early in September. This condition is attained some weeks before the fall drift starts and nearly two months before the breeding season begins.

Early in November and before the majority of deer have reached winter range, the rut begins. It is first evident among animals at 6500 feet or lower, and as the migration gets under way, it quickly develops to its height and continues well into December. In 1929, breeding began in October, which is unusually early. Normally, there is some breeding activity while the animals are enroute to winter range, but since most deer reach winter range before showing signs of the sex urge, I believe no necessary correlation between the two activities can be established. Table I shows the dates of breeding in the Yosemite region over a period of six years. Records for the Yellowstone region are inadequate for the preparation of such a table.

Evidences of the rut are unmistakable to one familiar with deer behavior. The bucks manifest a restlessness and a tendency to assume a pose which is strictly characteristic. In the presence of does, a breeding buck will repeatedly lower his head so as to lay his antlers back near his shoulders and stretch his neck to the utmost. The base of the skull is depressed, the tip of the nose elevated, and the nostrils distended. This posture of the head and neck is often maintained when trotting in pursuit of a doe as well as when standing. Not infrequently during the rut, bucks give voice to a low, deep-pitched *b-a-a-a*. This sound is especially apt to be uttered when the animal is maneuvering with a doe, impatient with a bothersome fawn or angered with a rival buck.

When intent upon a doe at rutting time, a buck is commonly quite oblivious to other affairs among animals or to human beings that may be near. It is evident that the sensitive nose of a sexually active buck can pick up the scent of a doe in heat, although this female may have passed from his locality some minutes before. Bucks habitually follow the trail of rutting does and, like a dog, with nose to the ground trace the tracks of the desired animal through

a maze of trails made by other deer. I have observed such pursuit to culminate in success for the buck after twenty minutes of blind trailing by scent through a half mile of fairly dense brush cover.

It would appear that does make no particular attempt to separate from their fawns during the rut. The incessant chasing to which they are subjected at this time results in great disturbance to their usually quiet daily routine, and instances have come to my notice of fawns being lost temporarily. In some cases, such separation occurred in families readily identified, and it was noted that a reunion of fawns and mother took place when the female no longer excited the attention of bucks. As a rule, however, the fawns race along with the beset mothers, and quiet family affairs are resumed after the rut. It is not until a short time before birth of fawns that the doe rids herself of the company of her young of the preceding year. Bucks intent upon serving a doe may become impatient with her ever-present fawns, and it is not unusual for them to make half-hearted lunges at the troublesome youngsters, but I have known of no truly purposeful attacks upon the offspring of a mate.

Conflicts between bucks are the exception rather than the rule. During the period of the hardening of the antlers, before the beginning of the rut, friendly wrestling matches between bucks are numerous. The contestants deliberately lock antlers and engage in rather strenuous bouts which may last, with intermittent breathing spells, for an hour. But when the period of actual breeding arrives, there is an evident careful hesitancy to engage in combat. Large bucks intent upon serving a doe encounter small opposition from other bucks. Small bucks in pursuit of a female yield to larger animals if their claim is disputed. I have witnessed but one true fight between breeding bucks among the thousands that have been under my observation. On this occasion, December 12, 1927, two eight-point bucks encountered each other near the foot of Yosemite Falls. No doe was in the immediate vicinity. The battle consisted of a series of terrific clashes launched when the animals were a few feet apart and interspersed with exhausting wrestling with antlers locked. One animal consistently gave ground to the other and at the end of five minutes turned tail and ran. But two other actual combats have been reported in Yellowstone or Yosemite during the eight year period that this study has been in progress (Michael, 1926).

Observations of actual coition are not as numerous as might be expected. But four instances of reports from eye witnesses were brought to the Yosemite Museum during my years there, and I failed to find a Yellowstone resident who had been witness to the act. It was not until the fall of 1930 that I was enabled to observe a buck cover a doe. The following notes are extracted from my Yellowstone field notebook:

"Nov. 14, 1930. This afternoon in driving to Gardiner I noted a number of deer in a state of agitation because of the activities of two amorous bucks.

They were but one hundred yards from the road, in open sagebrush country and nicely delineated against the eight-inch cover of new snow. I determined to secure pictures and rather deliberately set up the 6½" x 8½" view camera equipment. There were seven deer in the group. One fine eight-point buck devoted himself to a doe with a single fawn. A smaller buck was much interested in a doe followed by two fawns. The two groups, constantly moving because of the short rushes of the bucks, were some fifty yards removed from one another. Because of close proximity and absence of interfering vegetation, I selected the eight-point buck and his doe as subjects for the picture. The buck obliged by constantly assuming the pose so characteristic of the rut and made frequent rushes for the doe. She would evade him, as has always been the case with such does I have watched, and after a run of fifty yards or so return to the near vicinity of the station occupied when I began my observations. Occasionally, her trot would drop to a walk, which would permit the buck to nose about her tail. Her fawn of the year followed her constantly and was occasionally a hindrance to the buck, whereupon he would make half-hearted efforts to hook the young one with his antlers.

"I had watched this performance for about ten minutes, made two exposures, and put the camera in readiness for a third, when the doe, evading one of the sudden rushes of the buck, ran about thirty feet from him, with obvious kicking of heels and shaking of head not noticed in her previous escapes, and came to a sudden stop. She stood with her tail toward the buck and in evident expectation. He trotted up to her, head down, and without hesitation covered her. He remained upon her not more than four seconds, I think. I snapped a picture while he had her covered. The pair stood exactly broadside to me. I noticed no particular muscular movements of either animal during the act. The doe stood perfectly still. In fact, her attitude from the moment she stopped was that she anticipated the events that transpired. I believe the buck got off without her moving. Afterward, they remained near each other. The doe frequently lifted her tail in a manner not typical of the animal at other times, and a marked spasmodic contraction of the external genitalia was evident. The buck continued to follow when she moved short distances. The doe smelled about his nose, his antlers, and his tail in a caressing manner. There was no further intercourse during the additional fifteen minutes that I kept the pair under observation."

By the close of the rut in December or January, the bucks present a worn appearance, characterized by loss of flesh, dejected postures, and apparent stiffness of joints. A few weeks after the breeding period closes, antlers are dropped, and both males and females enter upon a period of quiet living upon the winter range.

FOOD HABITS

The following observations are based on notes taken in the Lamar-Yellowstone section. The variety of food available on winter range is much limited as compared with the numerous species of plants fed upon in summer. The most favorable areas of winter range experience minimum temperatures of -30° F., with mean temperatures of 0° not at all uncommon. Snow

on winter range is not excessive, five to fifteen inches being usual. High, persistent winds cause the snow to drift, so that numerous exposed slopes and elevations are swept quite clean. The deer seek out sheltered timbered coves in which to rest and at feeding time venture into deep snow to take advantage of sagging limbs of trees that have inclined under the weight of snow, or go out to exposed areas from which the snow has been blown away. Wm. Rush (1930) advances the idea that it is the condition of the crust of snow which determines distribution of elk, rather than the depth of snow. If snow is loose, he finds that elk remain at high altitudes in spite of low temperatures and deep snow. It has been my observation that the deer of Yellowstone do not so frequently paw through the snow for food as do the Yosemite animals, or as do the elk of Yellowstone.

COMPETITION WITH OTHER LARGE ANIMALS

In winter, Yellowstone deer come into direct competition with three browsing and grazing animals: mountain sheep, antelope, and elk. Buffalo constitute a fourth competitor in parts of the winter range. The same food plants sought by deer are hungrily consumed by the others (Bailey, 1930; Skinner, 1928). In primitive times, the animals of the park area descended to regions far removed from the present winter range and secured their food from areas of wide extent and ample capacity. Present day conditions of human occupancy of the old winter haunts prohibit such spreading. A fence through the present winter range and along the north boundary of the park tends to discourage the extended drift of the animals and, except in instances of very severe winters, serves to keep them within the bounds of national park protection. Recent investigations (Rush, 1931) indicate that food of the present winter range is not less nutritious than was the forage on the primitive range.

The congestion which results from the enforced limitation of drift overtaxes the natural capacity of the range and makes necessary the artificial feeding with hay. All of the large mammals participate in the benefits of such feeding and all of them have changed their normal habits accordingly. It is evident, however, that the supplementary feeding of hay has not greatly affected the natural feeding upon native plants, for this section of the park is consistently grazed and browsed upon to the point of near ruin. Plants observed to be fed upon in winter are: *Amelanchier alnifolia*, June berry; *Artemisia* (several species), sage brush; *Chrysothamnus lanceolatus*, rabbit brush; *Festuca* sp., fescue; *Juniperus scopulorum*, Rocky Mountain cedar; *Juniperus sibirica*, ground juniper; *Pinus flexilis*, limber pine; *Poa* sp., blue grass; *Populus tremuloides*, quaking aspen; *Prunus melanocarpa*, choke cherry; *Ribes cereum*, squaw currant; *Ribes viscosissimum*, sticky currant;

Rosa acicularis, wild rose; *Ribes setosum*, wild gooseberry; *Salix fluziatilis* and *S. pseudomyrsinites*, willows; *Stipa* sp., spear grass; and *Symphoricarpus occidentalis*, snow berry.

SPRING MIGRATION

For about five months the Yellowstone deer must contend with winter conditions of a severity not approached in the Yosemite region. These conditions are moderated in March, when mean temperatures steadily climb. In the vicinity of Mammoth Hot Springs, snow disappears in March or April. Exact dates of disappearance of snow during the three years that this study was in progress are 1928—April 10; 1929—March 27; 1930—April 2. The snow line rapidly retreats and by early May is usually near the 8000 foot contour line. It might be expected that deer would follow the ever-climbing snow line and so arrive on summer range at about the time that the Central Plateau was free from snow. This is not the case.

The advent of mild temperatures at the 6200 foot level during April brings about rapid development of new grasses. By April 15, an abundance of green forage is available on winter range. Important among these plants are: *Bromus* sp., brome grass; *Calamagrostis canadensis*, reed grass; *Festuca idahoensis*, fescue; *Panicularia nervata*, manna grass; *Poa pratensis*, blue grass; *Stipa richardsoni*, spear grass; and *Taraxacum ceratophorum*, dandelion.

This succulent herbage holds the deer to the scene of their winter difficulties until similar growth of new vegetation takes place at higher levels. Bucks tend to lead the way to new feeding grounds. The upward drift begins with a very gradual extension of daily movements and results in a scattering of the animals that during the winter had congregated in sections of the winter range. For more than a month after the disappearance of snow, however, deer remain at levels designated as winter range. A few elect to remain all summer. The true upward movement is coincident with the development of green vegetation at higher levels, and arrival on summer range does not occur for some twenty days after snow has melted from the 7500 foot level. These individuals that travel to the upper limits of summer range appear to climb very slowly from the 7500 foot level and do not appear at 8500 foot elevations for about a month after most of the snow has disappeared from these high elevations. By this time, the middle of June or later, spring has arrived on the heights. It is very evidently availability of food that regulates the spring migration in the Yellowstone country.

The condition of forage plants also affects the routes of travel. As an example of the influence of spring growth upon the path of migration, circumstances attending the movement of about 300 deer of the Mammoth-Gardiner-Mount Evarts winter range may be described. Two natural exits

exist which might be expected to serve as lanes of travel from the depressed basin in winter range. One route, via Snow Pass to the park plateau at Swan Lake, leads westward and necessitates a climb of 1500 feet in four miles. The other route, via Lava Creek and Crescent Hill, leads eastward (Mammoth-Tower Falls Road) and requires about fifteen miles of travel with the same ascent (1500 feet). Investigation shows that the longer route comes into use a week earlier than does the other and that a far greater number of animals, both elk and deer, follow the eastward route. In the spring of 1930, new growth of grasses and leaves of shrubs were noted to be well advanced in the vicinity of Crescent Hill (7500 ft.) on May 4. Examination of forage plants in Snow Pass (7400 ft.) on the same date showed that a moss in small streamlets was the only representative of green vegetation. The entire route from Mammoth to Crescent Hill afforded an abundance of new growth, while no spring growth was in evidence eight hundred feet below Snow Pass. On May 4, numerous deer were traveling toward Crescent Hill, and on May 7, a veritable migration was under way there. It was not until May 11 that the first deer went through Snow Pass. No conclusive evidence exists upon which to base the statement that deer would not first follow the Lava Creek route even though topographical conditions were such as to bring about uniform development of plants along both routes. It seems reasonable to conclude, however, that the earlier production of forage along the eastern route serves as an inducement to start a large percentage of the deer of the Mammoth region upon this longer way to summer range.

Data on the migration route of an individual Yellowstone deer have been provided by members of the park's ranger and educational staffs. In 1921, a buck, "Wheezy," demonstrated tendencies to become very friendly with members of the human population at Mammoth Hot Springs, within his winter territory. Because this animal was possessed of an unusual head, he came to be recognized by all residents. This intimate acquaintance, over a period of years, made possible significant reports on his seasonal movements. His summer range was near the Thumb on Yellowstone Lake. In leaving Mammoth in the spring, he journeyed by way of Lava Creek, Crescent Hill, Tower Falls, Dunraven Pass, and Canyon to Lake. This route is not less than fifty miles in length and probably more than sixty miles. In the fall, the same route was retraced. Unfortunately, no records were made as to time involved in making the journeys.

THE MULE DEER OF THE YOSEMITE REGION

Conditions of the Yosemite region range from the hot, dry slopes of the brushy foothills to the bleak regions of glaciers and perpetual snow on the mountain tops. The slopes are beautifully watered by springs, creeks, rivers, ponds, and lakes. Granite bosses, tremendous cliffs, glacial moraines, great

canyons, and rock-rimmed basins unite to give an irregular topography which provides southward-facing slopes bathed by long hours of sunlight and shady, moist north slopes little affected by direct sunlight. On the long gradual western slope of the Sierras, the mule deer are found in greatest abundance in summer within the beautifully timbered Canadian and Hudsonian Zones. In winter, the greater number of animals descend to the Upper Sonoran area, although some may remain in the Transition Zone, and a small percentage occupy the foothill belt, or Lower Sonoran Zone.

Sierra Nevada mule deer have received frequent casual mention in printed accounts of the region ever since Leonard's narrative of the 1833 Walker Expedition appeared in 1839, but truly significant accounts of the animal did not appear until very recent years. Grinnell and Storer (1924) have accorded the species a good general treatment, and more recently Grinnell, Dixon, and Linsdale (1930) have added a valuable account. Hall (1927) has published notes, many of which apply to the Sierra deer.

In Yosemite National Park, the mule deer constitutes one of the most interesting features of the area. It is present in surprising numbers and within the past ten years has so changed its habits as to be continually on exhibition somewhere within the park. The 1930 animal census from the park superintendent's office indicates a deer population of 16,000. I believe this number falls short of the total number of animals which inhabit the park in summer. Prior to 1925, no one would have estimated a Yosemite deer population of more than 5000. In 1924 and 1925, some 22,000 deer (actual count) were killed because of the epidemic of foot and mouth disease, which affected a part of the deer of the Sierras (Mohler, 1926). This regrettable happening at least provided authentic data upon which to base future estimates of deer numbers. Most of the slaughtered deer had resorted to the northern part of Yosemite National Park in summer. They constituted the so-called "Tuolumne Herd," and their summer range represented less than half of the available summer range within the park. There is no reason to believe that the Merced drainage system was less densely populated than was the Tuolumne. On the contrary, observations would indicate that a greater number of deer frequented the southern half of the park. During the four years that have elapsed since the Tuolumne herd was so nearly destroyed, the animals of the Merced region have greatly increased in numbers. The Tuolumne animals have "come back" slowly, and there can be no good basis of reasoning which would place the present Yosemite deer population at less than 30,000.

SUMMER RANGE AND SUMMER ACTIVITIES

An ever-growing number of Yosemite deer are responding to the influence of artificial conditions created by man and choose to remain in Yosemite

Valley (Transition Zone) the year around. Actually, this group of non-migrants represents a percentage of the total deer population that is hardly appreciable, and like a few deer that spend the entire year in the Upper Sonoran Zone, may be ignored in relation to the general applications of the present studies. Non-migrants are given further mention elsewhere in this paper. By far the greater number of deer of the Yosemite country travel to the Canadian and Hudsonian Zones (6200 feet to 10,500 feet) for the summer. The heart of this summer range lies about the 7500 foot level. Some deer, old bucks especially, frequent the bare granite ridges near timber line. During high-country studies, I have frequently come upon bucks in such situations. The greatest altitude at which I have found them is 10,000 feet on Tenaya Peak. Old bucks are not uncommonly accompanied by a younger male, and sometimes three males associate during their weeks on the heights. The highest Yosemite record (Grinnell and Storer, 1924) is 10,600 feet at Fletcher Lake.

The region of summer range is characterized by rounded prominences and shallow canyons forested with splendid stands of jeffrey pine and red fir. In certain areas the lodgepole pine, *Pinus murrayana*, predominates. Huckleberry oak and snow bush predominate in the brush cover. Quaking aspen, *Populus tremuloides*, occurs in groves of splendid trees and in dense thickets of brush and saplings. At the upper limits of summer range, jagged peaks and bare granite ridges replace the forested prominences. Just below these heights occurs the boreal forest of mountain white pine, *Pinus monticola*; white-bark pine, *Pinus albicaulis*; and alpine hemlock, *Tsuga mertensiana*. Willows, *Salix glauca villosa* and others; Sierra maple, *Acer glabrum*; dwarf manzanita, *Arctostaphylos nevadensis*; wormwood, *Artemisia norvegica*; and Labrador tea, *Ledum glandulosum* represent the shrubs of the ground cover.

REARING OF YOUNG

On the summer range, few enemies harass the deer, and the summer activities comprise carefree daily movements in an abundance of browse with successful family affairs, which nearly always result in each doe escorting two well grown fawns to winter range. The young are born in June or early in July, soon after the mothers arrive on summer range. In 1924, I found a new born fawn on June 15. T. J. Jones of the Inyo Forest, in his annual report of 1925, states that the first fawn observed by him that year was born June 20. G. S. Way of the Inyo Forest saw the first fawn of 1929 on June 4, and this constitutes the earliest record of the Yosemite region. Usual dates of arrival are later, as indicated in the following table, which is based upon my observation unless otherwise indicated and is included here in order to throw light on the period of gestation:

TABLE I. *Breeding Dates and Arrival of Young for the Yosemite Region.*

Years	First noted evidence of rut	Last noted evidence	First noted fawn	Last noted fawn
1923-24	Nov. 12	Dec. 31	June 15	July 17
1924-25	Dec. 12	Jan. 10	June 20 ²	June 26
1925-26	Dec. 10	Jan. 21	June 26	July 15
1926-27	Dec. 16	Jan. 25	June 21	July 15
1927-28	Dec. 1	Jan. 14	June 29	July 9 ¹
1928-29	Nov. 26	Feb. 20 ¹	June 4 ³	
1929	Nov. 28			

¹Reported by George M. Wright. ²Reported by T. J. Jones ³Reported by G. S. Way.

Most of these observations on birth of young were made among deer that did not migrate but spent the summer in Yosemite Valley. The family cares of such animals are not so effectively concealed from the thousands of human beings who swarm over the area, and reports of tiny fawns are repeatedly brought to the Yosemite Museum or to the Chief Ranger's office. One of the trials of the ranger department during the period of fawning is the prevention of thoughtless "kidnapping" of very young fawns by tourists, who find the cached infants near their camping sites and are at once moved to "save" the "helpless little thing" that has been "deserted" by its mother.

On June 21, 1927, I obtained my only opportunity to record observations on a newly arrived fawn within the true summer range, where the great majority of fawns are born, but where incidents relating to their early care are seldom observed because of the precautions of the mothers, the vastness of the territory, and the sparseness of the human population. I had arrived at Merced Lake (7200 ft.) and about sundown was investigating possible inhabitants of willow thickets adjacent to a remarkable open forest of aspen, which exists at the upper end of the lake. I walked noiselessly between the trees, avoiding the few bushes and taking advantage of the spongy humus which covered the ground. As I gained a position which enabled me to look into an embayment in the thickly-growing willows, I was accorded a splendid view, at a distance of forty yards, of a doe engaged in licking the coat of a very young fawn. The little animal's long legs were wobbly but strong enough to indicate that it was at least twenty-four hours old. Apparently, it had just nursed. I made no effort to approach closer but was not long unobserved by the mother, who caught my scent or noted some small movement and bounded noiselessly out of sight behind the willows. The fawn made one awkward leap and flopped to the ground as though shot. The leap had sufficed to bring its body under the cover of over-hanging leafless wil-

low stems, and its spotted brown coat caused it to be nearly invisible in the failing light. I walked up to it, and it made no move. Its eyes remained open, and there was no movement of eyelids. I touched it with my fingers, and it responded with but the slightest wince of hip muscles I had touched. I made no further effort to disturb it. Other very young fawns which I examined in Yosemite Valley (six in all) reacted to my investigations in much the same manner. The characteristic "freezing," together with protective coloration and evident absence of scent (usually even the metatarsal gland of a very young fawn has no odor) no doubt save many fawns from preying beasts that would otherwise make meals of them.

I attempted to locate a possible twin of the Merced Lake fawn but did not succeed. I saw no more of the mother. The next morning, soon after daylight, I looked for the fawn and its mother but found neither of them. It is rather surprising that the thousands of small fawns which are born in the Yosemite high country do not more frequently come under the observation of the park visitors who walk through their haunts, but the fact that they are seldom noted is good evidence that the does of the high country have not relaxed in their habits of caution as have the semi-domesticated animals that spend their lives among the human habitations in Yosemite Valley.

A female fawn a few hours old on June 30, 1927 weighed six pounds and two ounces. On July 10, 1928, Wright and Dixon weighed two fawns known to be twenty-four hours old. The female weighed six pounds, four ounces; and the male, six pounds, ten ounces. On August 9, 1930, a Yellowstone fawn, about two months old, was found to weigh forty pounds (dead weight). A Yosemite fawn, about four months old, was killed October 26, 1929 by jumping into a snag which penetrated its lungs. It weighed fifty-nine pounds and two ounces. Its stomach contained material weighing four and one-fourth pounds.

Yellowstone rangers have reported that fawns take forage plants in their second week. Hall (1927) states that deer of the Kaibab Forest Reserve take forage at the age of two weeks. I have been unable to observe Yosemite fawns taking plant food at this age. For about one month, Yosemite fawns do not follow their mothers in the day time. Tiny tracks in the sands of lake shores and stream banks indicate that very young fawns accompany the mothers to drinking places at night, and it is probable that they move about with the does rather freely under the cover of darkness. In Yosemite Valley, where semi-domestication has resulted in a change of habits and lessening of vigilance, fawns quite commonly follow the mothers when six days old. I have watched these active youngsters carefully in an attempt to discover at what age they take plant food. I have seen no fawns that I could judge to be younger than one month attempt to browse or graze. Those that have been watched when making their first attempts to take such food have

always evidenced an awkwardness and doubt which suggest no avid appetite.

During the period of early development, fawns have little strength. As has been stated, they remain in concealment during hours of daylight and are probably more active at night than is generally supposed. Summing up personal observations made over a five-year period in Yosemite, I conclude that the mothers frequent the immediate neighborhood in which the young are hidden and come to the cached infants twice during hours of daylight to permit them to nurse. These visits occur anytime during a two hour period before midday and again during the late hours of afternoon. The does apparently make no attempt to keep in sight of the fawns' hiding places. Fawns more than a week old are with the mothers during many hours of the night and perhaps nurse more frequently than in the daytime. After attaining an age of five weeks, the fawns begin to take a considerable quantity of forage, but continue to nurse until the last of September. After this time, the does are reluctant to nurse them, but fawns frequently show a rough insistence upon mouthing the mother's teats even during the breeding season in late November.

In Yosemite, the spotted coat of the fawn begins to disappear in August and by the close of September has been replaced by a gray coat, which is often characterized by an abundance of long silky hairs not evident in older animals.

FOOD HABITS

The west slope of the Sierra Nevada, so much of which is occupied by deer, is abundantly watered and produces a great variety of flowering plants. No less than 1200 species and subspecies occur in the Yosemite region, and among these the deer find a wide variety of forage. On summer range, fifty per cent of the food taken comes from a half dozen species, but about forty others are very commonly eaten, and the complete list of plants known to be fed upon includes about one hundred species. Continued study would, no doubt, add many others to the list. Buds, twigs, soft fruits, and seeds and roots, as well as leaves, find places in the deer's diet.

Following is a list of all species of plants known to be fed upon in summer. The list is divided into two groups: those known to be commonly eaten, and those thought to be less frequently partaken of. It is based upon my personal observation, the reports of Yosemite ranger-naturalists, the notes of Dr. H. C. Bryant (Hall, 1927), and J. Dixon's (1928) published records. Names are based on the usage of Jepson (1925).

The following plants are commonly eaten: *Amelanchier alnifolia*, western service berry; *Arctostaphylos nevadensis*, dwarf manzanita; *A. patula*, green manzanita; *Calochortus nudus*, Sierra star tulip; *C. nuttallii*, Mariposa lily; *Ceanothus cordulatus*, snow brush; *C. integerrimus*, deer brush; *C. prostratus*, mahala mat; *Chenopodium album*, white pigweed (lower limits of

summer range; introduced); *Cornus pubescens*, creek dogwood; *Erigeron coulteri* and *E. ursinus*, flebanes; *Festuca elatior*, meadow fescue (European); *F. supina*, fescue; fungi, various species; *Helenium bigelovii*, Bigelow sneezeweed; *Lotus oblongifolius*, hosackia; *L. torreyi*, meadow hosackia; *Lupinus breweri* and *L. lyallii*, lupines; *Notholcus lanatus*, velvet grass (European); *Populus tremuloides*, aspen; *Polygonum alpinus*, knotweed; *P. aviculare*, wire grass (lower limits of summer range; European); *P. imbricatum* and *P. minimum*, knotweeds; *Prunus emarginata*, bitter cherry; *Quercus kelloggii*, California black oak; *Rubus parviflorus*, thimble berry; *Rumex crispus*, curly dock (European); *R. paucifolius*, dock; *Salix glauca* and *S. jepsoni*, willows; *S. petrophila*, alpine willow; *S. phylicifolia*, var. *monica*, Mono willow; *S. scouleriana*, Nuttall willow; *S. sitchensis*, var. *coulteri*, velvet willow; *Saxifraga integrifolia* and *S. punctata*, saxifrages; *Sorbus sitchensis*, western mountain ash; *Taraxacum* sp., dandelion; *Trifolium breweri*, forest clover; *T. longipes*, clover; and *T. monanthum*, carpet clover.

The following plants are known to be eaten occasionally: *Achillea millefolium*, common yarrow; *Agropyron* sp., wheat grass; *Agrostis* sp., bent grass; *Antennaria rosea*; *Aster yosemitanus*, Yosemite aster; *Calamagrostis* sp., reed grass; *Carex* sp., sedge; *Castanea sempervirens*, bush chinquapin; *Chrysothamnus bloomeri*, rabbit brush; *Cirsium acaulescens*, thistle; *Eriogonum nudum* and *E.* sp., fleabanes; *Festuca* sp., fescue grass; *Fragaria virginiana platypetala*, wild strawberry; *Geranium incisum* and *G. richardsonii*, geraniums; *Hieraceum albiflorum*, hawkweed; *Juniperus occidentalis*, Sierra juniper; *Lupinus covillei*, lupine; *Phleum alpinum*, timothy; *Poa* sp., blue grass; *Potentilla fruticosa*, shrubby cinquefoil; *Quercus vaccinifolia*, huckleberry oak; *Ranunculus alismaefolius*, butter cup; *Ribes cereum* and *R. montigenum*, currants; *R. nevadense*, Sierran currant; *R. viscosissimum*, currant; *Sambucus racemosa*, red elderberry; *Sarcodes sanguinea*, snow plant; and *Symphoricarpos creophilus*, snowberry.

Observations indicate that the following of the plants just listed are most eagerly eaten in the densely populated section of summer range (6500 ft. to 8000 ft.): *Arctostaphylos patula*, *Ceanothus cordulatus*, *Ceanothus integririmus*, *Cornus pubescens*, *Helenium bigelovii*, *Lotus torreyi*, *Populus tremuloides*, *Prunus emarginata*, *Rumex paucifolius*, and *Salix*.

Late in September and throughout October, the Canadian Zone (6200 ft. to 8500 ft.) experiences consistent frosty nights, which bring about changes in vegetation typical of fall. *Salix*, *Cornus*, *Quercus*, *Rubus*, *Ribes*, *Sambucus*, and *Castanea* are the first to turn color. *Ceanothus cordulatus* persists in its green color in spite of the lengthy period of frost, and deer continue to depend upon it for a major part of their forage. They do, however, partake of brown leaves of many species of their usual food plants and may be observed to feed on fallen leaves, as well as those that adhere to bushes and trees. Grasses at this time exist as green blades deep within the matted

dead tussocks which cover the meadows and swales, but there seems to be little attempt made by deer to secure green grass. A surprising tendency prevails to feed upon woody parts of such shrubs as *Salix*, *Manzanita*, *Ribes*, and *Prunus*.

The stomach of a fawn about four months old, killed near Bridal Veil Creek at an altitude of 7000 ft., October 26, 1929, was found to contain food weighing four pounds, four ounces. A rough classification of the contents gave the following proportions:

Finely macerated material, leaves, etc. not recognizable.....	73%
Coarse wood material, bark, stems, roots, species not recognized	22%
Remainder	5%
<i>Hieraceum albiflorum</i> , hawkweed, leaves.....	trace
<i>Ceanothus cordulatus</i> , snowbush, leaves.....	"
<i>Arctostaphylos patula</i> , green manzanita, leaves.....	"
<i>Salix</i> sp., willow, green leaves.....	"
<i>Salix</i> sp., willow, dry brown leaves.....	"
<i>Ribes viscosissimum</i> , currant, leaves.....	"
<i>Evernia vulpina</i> , staghorn lichen.....	"

FALL MIGRATION

During September and October, the summer coat of "red" is shed and replaced by the winter "blue." The molt of bucks tends to precede the change in does. By the middle of October, fawns of the year usually have produced their first winter coat, and summer spots are no longer to be seen. Some deer move to winter range while still in summer pelage, but a greater number undergo the molt while on summer range.

Records kept over a four year period reveal that the downward drift from the central summer range (7500 ft.) may start in advance of snow fall but that a part of the deer population usually remains at this level after precipitation of several inches of snow occurs and deserts these localities only after severe snow storms which quite cover food plants. Dates of the beginning of the fall drift (7500 ft. or thereabouts) range from October 10 (1928) to November 5 (1929). In nearly all instances, the downward movement from the central summer range is initiated by a snow storm. It is usual, however, for the drift of those animals that have summered at upper limits to begin without the stimulation provided by snow fall, and similar movements in advance of storms may occur among animals of lower levels. In 1929, many of the deer at Glacier Point (7200 ft.) and similar localities within the central summer range began their fall migration about October 25, more than a month in advance of the first snow storm. On that occasion, a part of the deer population slowly descended a thousand feet toward winter range. Snow storms of December 10 resulted in a precipitous rush to lower levels. For

purposes of comparison, this irregular instance is not a serious handicap in drawing conclusions, for hundreds of deer about the Glacier Point region remained on the central summer range as usual and delayed their descent until the coming of the snow storm of December 10.

Unless the early snow storms are of a severe nature, covering all zones to the normal lower limits of the snow line just below 4000 feet, the fall drift is not an impulsive rout. The first storms of the season usually result in a few inches of snow cover above 7000 feet, with greatest depth of snow at the higher levels of summer range. Any deer which may then be at 8000 feet or higher will start their migration to more favorable localities. Their descent through the belt of deepest snow will be steady and persistent. On the Glacier Point Road, during such a movement, I observed an identifiable buck travel in one hour a distance the shortest route of which would have involved five miles of travel. When a level has been reached, which permits of feeding without the encumbrance of snow, the march is delayed. If the browse of the locality is inviting, the animals will linger, and the feeding movements may result in little or no descent. If a period of warm weather follows the snow storm and the snow line is caused to retreat, the animals will in some instances ascend to slightly higher levels. No case has come to my notice in which Yosemite deer climbed more than 500 feet while en-route to winter range. It appears that the instances of animals making ascents while the fall migration is in progress result from daily feeding movements. If forage is more desirable on slopes some few hundred feet above, a movement results which takes the animal to that feeding area. The fact that upward movements, involving any great change in altitude, are exceptional during migration indicates that they are not brought about by a desire to maintain altitude merely, nor an urge to remain in proximity to the snow line. It is the presence of available food which controls the daily movements of migrating individuals just as it is the availability of food which regulates the mass movements of the deer herds of a region.

DETAILS OF MOVEMENTS

The following entry in my Yosemite field notebook is pertinent here:

"November 22, 1929. Visited the area above Chinquapin traversed by the Glacier Point Road. In the Indian Creek drainage basin, at an altitude of slightly more than 7000 feet, I found several dozen deer—does, fawns, and bucks. Some of the animals showed unmistakable evidence of intimate acquaintance with man; others were extremely shy. It is reasonable to believe that the approachable individuals had traveled from the vicinity of camp sites on the Glacier Point Road, some miles distant, and that the wary animals had descended from regions unfrequented by tourists about the headwaters of Bridal Veil Creek.

"The slopes about Indian Creek, which on October 15 were not densely populated with deer, were literally cut up like a barn yard. The animals seen

today were a part of the great "drift" that is making, or has already made its way to winter range. I remained in one neighborhood for four hours. The unhurried movements of all deer involved in the migration further substantiate the idea that the animals move down from summer range very leisurely if they are not hurried by storms. Feeding progressed in a normal manner, and with the exception of one doe, followed by two fawns, who stepped along with an apparent intention of making definite progress to lower levels, there was nothing about the movements of the animals to indicate that they were enroute to winter range. Yet a study of the maze of new trails through the *Ceanothus* indicated that very few tracks pointed uphill. The movements of individuals, deliberate though they be, result in a definite descent through a period of some hours. I found that scores of trails on the slopes picked their way along the auto road, which here passes through the canyon. Eight major trails, roughly parallel, were readily recognized (See Fig. 2). The general condition of the terrain suggests the passage of a thousand sheep, and it is evident that this shallow canyon provides a favorite route of descent from the high meadows and basins of the southern end of the park."

A special effort was made to determine relationships of food of summer months to the food taken while enroute to and after reaching the winter habitats. During a typical but decidedly active period of migration in 1929, I devoted three days, Nov. 21, 22, and 23, to studying the feeding habits of migrating deer along routes that were readily accessible from the Glacier Point Road. Data on summer food had been accumulated, as already described in this paper. Studies of winter food had been made over a period of five years and are described in succeeding sections of this paper. After considering details of feeding habits during the drift, I prepared the following summary as a record in my note book:

"Each day of the study I observed fifty or more deer enroute to winter range. Ninety-two per cent of the animals seen to feed took leaves and twigs of *Ceanothus cordulatus*. Eighty per cent of all animals sought the vicinity of, or entered thickets of *Ceanothus cordulatus*. They were either feeding or moving very slowly. The remaining twenty per cent frequented small open meadows, moved slowly without apparent purpose beneath the firs, or descended the more abrupt slopes of canyon walls. *Ceanothus cordulatus* in this section is one of the most prominent species of the chaparral and is nearly continuous from the 8000 foot level to 6000 feet. Just above the Chinquapin Station, it is replaced, imperceptibly, by *Ceanothus integerrimus*, *C. parvifolius*, and *C. prostratus*. On the south facing slopes, immediately below Chinquapin Station, conditions are such as to provide good winter deer range at 5000 feet to 5500 feet. Here *Ceanothus integerrimus* and *C. parvifolius* prevail. Along this migration route (Bridal Veil Meadows—Peregoy Meadows—Indian Canyon—Chinquapin), food plant conditions are quite uniform from the 8000 foot to 6000 foot levels. Within this belt the deer have slowly descended until many of them now (November 23) are at its lower margin; yet, it has not been necessary for them to change their diet greatly. The localities in which they are present in greatest numbers are im-

mediately above especially favorable areas to which they may descend in an hour should storms make such descent necessary or desirable."

For two weeks after these studies were made, I watched or had someone watch the deer of the section in question. On December 10, three inches of snow fell in regions above 6500 feet. Indian Canyon fairly spewed deer. Three days later, no deer were to be found about Bridal Veil and Peregoy Meadows, and but one young buck could be noted in the canyon of Indian Creek. In the logged-off basins below Chinquapin and just outside of the park (5000 feet), the animals flocked like sheep.

INSTANCES OF ABSENCE OF SEASONAL MIGRATIONS

It is common knowledge that the entire mule deer population of some regions habitually occupies a common winter and summer range (Seton, 1927). Grinnell and Storer (1924) point to the fact that some animals of the Yosemite region spend their entire existence in the Upper Sonoran chaparral belt. They express the belief that fawns born at low altitudes remain there throughout their lives, while those born in the mountains migrate with the change of seasons, thus implying that the habit of migrating is transmitted to successive generations through the teaching by mothers of experience. In the present paper, attention has been called to the non-migration of a part of the Yosemite deer (p. 19).

The numbers of deer occupying the areas in question are bound to be controlled by the food available. When numbers in any locality tend to become larger than the supply of forage will support, competition results in extension of daily movements of enough of the animals to relieve the pressure. In such areas as the chaparral belt west of Yosemite National Park, such extension of range is easily accomplished in either summer or winter. The idea at once suggests itself that in this competition there is the basic explanation of the origin of the migratory habit (Adams, 1919).

WINTER RANGE AND WINTER ACTIVITIES

Areas west of the summit of the Sierras to which park deer resort in winter vary in altitude according to exposure. These California animals are not forced to contend with severe winter conditions as are the Yellowstone deer and they take full advantage of their opportunities to secure favorable winter abodes. Prominences which slope south and east may, during most of the winter, afford ideal conditions at altitudes of 5000 feet or slightly higher. Such conditions prevail in the Merced Canyon above El Portal and in many places upon the slopes of the basin drained by the South Fork of the Merced and its tributaries. After snow accumulates to the great depths that are usual in February and March, there are few areas above 4000 feet in which the deer find conditions suited to their winter existence. They then descend to regions

about the snow line, which, for the purposes of this paper, has been defined as 3000 feet. The deer of Yosemite Valley constitute exceptions in this movement. When the writer's studies were begun in 1923, very few animals remained in Yosemite Valley in winter. During the years of my residence there, I was enabled to observe a marked change in habits among the animals that frequented the Merced Canyon and wintered below Yosemite Valley. The number of deer that inhabits the Valley, both summer and winter, has increased noticeably each year, until at present a true congestion exists there in winter, which is little relieved even on occasions of heavy snow storms. The deer of this particular locality no longer desert the 4000 foot altitude when food plants are deeply buried, because they have come to regard the "back-door hand-outs" of Yosemite villagers as a reliable food supply. As a matter of fact, they partake of quantities of garbage at all times, regardless of snow depth, and persistent feeding in this manner, together with the general let-down in vigilance resulting from continued life among human residents, has made of them a sodden group, which contrasts greatly with the graceful alertness of the normal animals not so closely associated with human affairs. It should be remembered, however, that the several hundred deer of such modified habits represent less than one per cent of the total deer population of the park.

Grinnell and Storer (1924) found that winter range extended westward from Yosemite National Park to include regions as low as 1500 feet. The Yosemite map (Fig. 3) shows clearly the relationship of winter range to the park area but is not large enough to include all winter range known to be available in the region. Conditions within much of the winter area west of Yosemite are typical of the Upper Sonoran Zone. Chaparral, including such species as mountain mahogany, *Cercocarpus parvifolius*; western red bud, *Cercis occidentalis*; poison oak, *Rhus diversiloba*; California buckeye, *Aesculus californica*; manzanita, *Arctostaphylos mariposa*; sagebrush, *Artemisia tridentata*; and wedgeleaf ceanothus, *Ceanothus cuneatus*, covers the dry rolling prominences or blankets the precipitous canyon sides. Ample cover is provided by this dwarfed forest, and except in regions overrun by stock, affords an abundant food supply. The digger pine, *Pinus sabiniana*, and the interior live oak, *Quercus wislizenii*, make a feeble show at foresting the region.

As long as snow conditions permit, many of the deer do not enter deeply into this belt but remain near the edge of the Transition Zone, where they occupy the yellow pine forest (*Pinus ponderosa*) and feed on their favorite browse, the deer brush, *Ceanothus integerrimus*. Upper limits of winter range are clearly defined by snow depth. If a period of mild weather causes shrinkage of the snow cover, deer immediately take advantage of the opportunity to move into the heart of the Transition Zone. Winters at middle alti-

tudes in the Sierras are not infrequently mild, but it should not be understood that regions above 5500 feet are commonly free from snow during winter months. Up to this limit (5500 feet), however, deer may be found whenever snow conditions permit.

The winter range of mule deer inhabiting eastern slopes of the Sierra in the Yosemite region differs greatly from that described for the western slope. It occupies mountainous country 7000 feet to 8000 feet above sea level and experiences winter conditions of a severity to be compared with that of the Yellowstone country. The limits of this range indicated on the accompanying map have been supplied by Supervisor Roy Boothe of the Inyo National Forest and Supervisor W. M. Maule of the Mono National Forest.

Mr. Maule, writing me under date of Nov. 7, 1930, states:

"It is quite evident that the summer range of these deer extends some miles over the Sierra summit to the west and the line dividing summer and winter range is roughly that of the merging of the single-leaf pine with the Jeffrey pine. This line, of course, is primarily determined by climatic conditions which affect the peculiar vegetative types. There is an intermediate zone lying partly within the two types in which the deer winter and this occupied area varies with the character of the winter, passing farther eastward during periods of heavy snowfall.

"Within the area I have indicated as winter range (See Fig. 3), one finds tracts of high mountains whose midwinter snows force the deer to lower altitudes where the living conditions are more acceptable or possible. Within this winter area, also, the deer are required to compete with quite a population of sheep which graze over the more accessible portions while the deer are restricted to the more rugged canyons or are held to certain timbered areas which offer them forage which is not relished by the sheep. This latter includes the nuts of single-leaf pine and mountain mahogany twigs.

"I have frequently found cases where deer have "yarded" among thickets of bitter brush, *Kunzia tridentata*; it seems that these instances have been due largely to the deer having been caught in heavy storms and were unable to find their way to the more snow-free areas."

BREEDING

Evidences of the rut are first to be observed among the animals on winter range. Breeding dates have already been given under "Rearing of Young." Without exception, the earliest breeding activity was noted to occur among those animals which had spent the summer at low levels, or among the first arrivals from summer range. Some breeding takes place among deer enroute to winter range, but I have never seen evidence of the rut in animals that had not descended below the heart of summer range.

The breeding activity in Yosemite is in every way similar to that in the Yellowstone, except that it occurs three weeks or a month later. In general, it may be said that this is consistent with the later dates of fall migration in Yosemite. The mad racing of both sexes at this time is quite as described for the Yellowstone region, and further account of breeding affairs would but

repeat what has already been stated. One note relative to the age at which bucks manifest the breeding instinct seems worthy of place here and is quoted from my Yosemite notebook:

"Jan. 2, 1925. At 8:00 a. m. I went to old Camp Lost Arrow to make observations on breeding deer. I found the animals still very active and was especially impressed by a little buck with spikes not more than four inches long. He appeared to be beside himself with the mating desire and determined to secure an eligible doe that was attended by a six-point buck. When the young buck would approach the doe, he was immediately chased away by the big buck, and for one and one-half hours the older animal was kept in a state of distraction. Such mischievousness, however, was not the youngster's main objective. It was evident that in spite of his age (he could not have been more than eighteen months old), he was ready to breed. Finally, after many attempts to get close to the active doe, he humped his back and projected his penis some six or seven inches from its sheath. It moved spasmodically, dorso-ventrally, a few times, after which the buck turned his head and licked the organ with his tongue. It then disappeared. There was no evidence of an emission."

It is likely that such sexual activity in so young a buck was an instance of precocity, for at no other time were very young males noted to manifest so evident an urge to breed.

FOOD HABITS

As has been pointed out, the west slope Transition and Upper Sonoran Zones in which Yosemite deer winter do not experience extremes of temperature or heavy snowfall, which characterize the severe winters in the Yellowstone. Sub-zero temperatures are unusual, and daily mean temperatures of less than 35° F. are unknown. Days of warm sunshine prevail, and snow accumulates to no great depth. Food plants are present in abundance and in a palatable condition. Cover is ideal, and few enemies exist. The hunting season extends from September 16 to October 15 and comes at a time when the great part of the Yosemite animals are safe within the limits of the park. In general, it may be said that winter range adjacent to the park, in its present condition, is a veritable deer paradise. Possibility of serious change in the existing favorable conditions (Brown, 1929, ms.) constitutes sufficient reason for extending the park boundaries to include winter range.

Food plants known to be eaten are: *Arctostaphylos mariposa*, Mariposa manzanita; *Artemisia vulgaris*, sage brush; *Ceanothus cuneatus*, buck brush; *C. integerrimus*, deer brush; *Cercocarpus parvifolius*, mountain mahogany; *Cirsium californicum*, Sierra thistle; *Cornus californica*, creek dogwood; *C. Nuttallii*, mountain dogwood; *Erigeron canadensis* (eastern United States) and *E. virgatum*, horseweeds; *Festuca elatior*, meadow fescue grass; *Garrya fremontii*, bear brush; *Holcus lanatus*, velvet grass; *Libocedrus decurrens*, incense cedar; *Lotus americana*, Spanish clover; *Oenothera hookeri*, evening

primrose; *Phoradendron villosum*, common mistletoe; *Populus trichocarpa*, black cottonwood; *Prunus demissa*, western chokecherry; *P. subcordata*, Sierra plum; *Pteris aquilina*, common brake; *Quercus chrysolepis* (also acorns), canon oak; *Q. kelloggii* (also acorns), California black oak; *Q. wislizenii*, interior live oak; *Rhamnus californica*, coffee berry; *Ribes quercetorum*, gooseberry; *Rosa californica*, California wild rose; *Rubus leucodermis*, wild raspberry; *Rumex acetosella* (European), sheep sorrel; *Salix lasiandra*, yellow willow; *Sambucus velutina*, elderberry; *Symphoricarpos racemosus*, snow berry; and *Umbellularia californica*, California laurel.

Of these, the following are of greatest importance because of their occurrence in quantity and their apparently greater relative palatability: *Arctostaphylos mariposa*, *Ceanothus cuneatus*, *Ceanothus integerrimus*, *Cornus californica*, *Festuca* sp., *Libocedrus decurrens*, *Prunus demissa*, *Quercus chrysolepis*, *Q. kelloggii*, *Rosa californica*, and *Salix* sp.

It is seldom that the snow cover of the 3000 to 4000 foot belt persists after March 1. As has been explained, a great number of the animals stay in close proximity to the snow line through the winter months and with rapid shrinking of the snow in the spring make their way upward, keeping pace with the retreat of snow. Above 6000 feet, climatic conditions are such that the melting of snow is retarded, and regions above this level are seldom free from snow before May 1. As a consequence, the deer may leave winter range but do not at once succeed in occupying summer range. They are present in numbers in the zone between 4000 and 6000 feet during the months of March and April. In this respect, the spring migration in Yosemite differs notably from the same movement in the Yellowstone region, where because of food advantages, the deer remain on winter range for some six weeks after the zone immediately above winter range is free from snow. The explanation seems to lie in the fact that the Yosemite plants of the middle altitudes leap into the spring state with a rapidity not possible under Yellowstone conditions. Grasses and other herbaceous plants produce green shoots immediately after snow melts. Some of them remain green all winter and take an important place in the winter diet. *Arctostaphylos mariposa* and *Ceanothus cuneatus* sometimes burst into bloom while surrounded by snow.

SPRING MIGRATION

The favorable state of forage plants having induced the deer to ascend with the upward retreat of the snow line, the first of May usually finds a considerable deer population in regions as high as 6000 feet. Above this level, snow does not disappear so rapidly, and when it does melt, low temperatures prevail which serve to retard plant development. As a consequence, deer do not rush into the area as they did when occupying the 4000 to 6000 foot zone. In this stage of the upward movement, the features of spring migration are much like the Yellowstone spring drift. Deer remain at those levels where

palatable food is most abundant and, when spring conditions have affected higher regions, they travel upward at a deliberate rate which fairly keeps pace with the development of plants. Routes are the same as those followed in the downward drift.

Arrival in the heart of summer range (7500 ft.) is usually three weeks or a month after the greater part of the snow of that level has disappeared. By this time (June 1 to 15), forage has attained a state of development attractive to the animals, and they enter upon the normal existence of summer. Those individuals that seek higher feeding grounds (more bucks than does) succeed in reaching the upper limits of summer range (9000 ft.) two or three weeks (July 1 to 15) after arrival on the 7500 foot level.

The spring molt occurs in May. No instance of a Yosemite deer arriving on summer range in the winter coat of "blue" has come to my notice.

A unique opportunity to study the seasonal movements of a mule deer of the Sierras was provided when a bell was placed on a Yosemite doe. (Russell, 1925). For nearly a decade, this animal was under observation and provided definite evidence as to what constitutes a migration route. It has been generally assumed by the inhabitants of the Sierras that deer regularly follow the same route year after year and consistently occupy the same range. In this instance, that belief has been substantiated so far as concerns the route of travel. The doe in question has always wintered in the Merced Canyon at Cascades (3500 ft.) or Yosemite Valley (4000 ft.). During the first years that she was under observation, her summers were spent in Little Yosemite Valley (6200 ft.), but in 1929 she was seen to ascend the Merced to its very headwaters and spent at least a part of the summer near the summit (10,000 ft.) of the range. On that occasion, she was not accompanied by fawns, as was always the case during her summers in Little Yosemite. The maximum distance traveled was about forty miles, with an altitudinal change of 6500 feet. While the destination at either end of the journey varied, this doe did not show an inclination to leave the Merced drainage system. In fact, her route was invariably the same between Cascades and Washburn Lake, a distance of about twenty-five miles. This is to be expected since the most accessible route is here much limited by the canyon of the Merced.

Mountaineers, generally, maintain that deer do not pass from one drainage system to another. After the destruction of the "Tuolumne Herd," because of foot and mouth disease in 1925-1926, it was hoped by some officials that deer from the adjacent Merced drainage system would repopulate the Tuolumne region of the park. No evidence of such a movement of deer could be noted. In 1929 and 1930, deer from the Merced drainage basin were captured and transported to the Tuolumne. What the seasonal movements of the transplanted animals may have been has not been observed.

Excellent opportunities exist in both Yellowstone and Yosemite to carry

on marking experiments and so accumulate more evidence regarding migration routes, speed of travel during migration, and home territory. The organization of the system of general ecological studies in the national parks which is now contemplated should embrace such experiments.

DISCUSSION

RELATION OF SEASONAL MOVEMENT TO BREEDING ACTIVITIES

Accumulated evidence presented (pp. 12, 29) points to the conclusion that in both the Yellowstone and Yosemite regions, breeding does not take place among migrants while they are on summer range. In the geyser basin region of Yellowstone, where some deer do not migrate, breeding occurs at high levels generally regarded as summer range. Breeding in the Yosemite country usually occurs two weeks later than in the Yellowstone region, and in both sections the earliest breeding takes place at the lower levels. As the season progresses, some animals enroute to the winter range may show evidences of the rut, but by far the greater number of deer reach winter range before becoming sexually active. It may be stated that breeding is coincident with arrival on winter range. Since nonmigrants of the geyser basins on the high plateau of Yellowstone Park breed at normal dates, no evidence can be produced showing breeding to be a causative factor in the seasonal movement.

RELATION OF MIGRATION TO BIRTH OF YOUNG

In Yellowstone Park, fawns are born in June or early July. Does heavy with young make the journey to summer range with other migrants and arrive there a few days or a few weeks, according to the season, prior to birth of the young. The Yosemite breeding dates tend to average from a few days to two weeks later than the Yellowstone dates, and birth of young is slightly later accordingly (p. 20). The period of gestation is ordinarily regarded to be seven months. Hall (1927) gives it as six and one-half or seven months. Migrating does of Yosemite National Park arrive on summer range but a few days or a few weeks before giving birth to young.

The question may arise, "Do does seek higher levels in order that their young may benefit by certain favorable conditions of the upper zone?" I think this may be answered in the negative, as no evidence exists indicating that Canadian and Hudsonian conditions offer anything advantageous to fawns. In the Yellowstone, elk sometimes descend to lower levels to give birth to young and, when the calves are strong enough, return to summer range. This habit has not been observed among the deer, but such behavior of elk indicates that summer range offers no particular advantages to the very young of either animal.

Fawns born at 4000 feet or lower evidently do not migrate. Fawns born on any part of the true summer range accompany the mothers all summer and

are escorted by them to winter range in the fall. It is usual for the family group to remain together through the winter (except for possible separation during a few days at the time of the mother's breeding period) and, as a group, to make the ascent to summer range the next spring. Upon the arrival of a new family, the yearlings are driven away by the mother.

A nice correlation exists between birth of young, rearing of young, and seasonal migration, but only in so far as it is a fact that the young are shown the routes of travel by the experienced mother can the relationship be shown to be of a causative nature.

RELATION OF MIGRATION TO CLIMATOLOGICAL PHENOMENA. TEMPERATURE

In both regions, the upper limits of summer range (Yosemite, 9000 ft.; Yellowstone, 8500 ft.; see Figs. 4, 5) experience mean temperatures of 30° to 40° F., with minimum temperatures of 5° to 20° F. quite usual. Deer of these high levels react to the drop in temperature, or to the change in food plants which results from the low temperature, and manifest a tendency to move to lower parts of the summer range. This is the beginning of the fall migration, and in the Yosemite country, it may precede snow storms by as much as two months. In the Yellowstone region, it may or may not precede snow storms (p. 11). September snow storms in that part of the Rocky Mountains are not unusual, and the first fall movements of deer of high levels are usually coincident with snow fall.

Minimum temperatures of 32° F. result in marked changes, external and internal, in forage plants. To what degree this change in forage conditions is responsible for the first movements of the deer of high levels cannot be determined, but very evidently a correlation exists.

In the middle regions of summer range, initial fall movements (one exception during the course of this study, p. 24) are delayed in spite of drops in temperature and changes in food plants, until snow storms occur.

In comparing daily mean temperatures of the Yellowstone central winter range (6200 ft.) at the time of the beginning of the spring migration (Figs. 4, 5), one finds that mean temperatures vary from 37° to 47° F. (1928, 45°; 1929, 37°; 1930, 47°; see Table II). Mean temperatures of the central summer range at the time of beginning of the fall migrations vary from 24° to 31° F. (1928, 24°; 1929, 31°; 1930, 28°). In the spring, daily mean temperatures of the summer range at the time of arrival of deer vary from 41° to 45° F., and in the fall, mean temperatures of the Yellowstone central winter range vary from 16° to 23° F. Comparison of these data with similar data for the Yosemite region (Table II) indicates that mean temperatures at times of migration vary much as they do in the Yellowstone country, but that higher temperatures prevail in the Sierras when migrations take place.

TABLE II. *Comparison of Daily Mean Temperatures at Times of Deer Migrations Figures indicate the mean temperature in degrees Fahrenheit at the time of arrival of deer at 6500 and 7800, or 4000 and 7000 foot levels, and of departure at the 6200 or 3000 foot levels.*

YELLOWSTONE

Elevation	Spring Migration			Fall Migration		
	1928	1929	1930	1928	1929	1930
6200'	45°	37°	47°	22°	23°	16°
6500'	45°	36°	42°	17°	27°	21°
7800'	45°	39°	41°	24°	31°	28°

YOSEMITE

Elevation	Spring Migration			Fall Migration		
	1927	1928	1929	1927	1928	1929
3000'	58°	62°	53°	42°	51°	47°
4000'	59°	63°	57°	40°	48°	45°
7000'	53°	54°	46°	42°	38°	43°

SNOWFALL

Early snow storms have a marked effect on deer on summer range (Figs. 4, 5). In Yellowstone, the central plateau region experiences freezing temperatures in September, and animals manifest a restlessness at this time which results in indefinite extension of daily movements. A notable number of animals begin their travel toward winter range when the first snow storms occur. These first movements may carry the animals slowly over a route of some twenty to fifty miles, all of which may be at levels regarded as summer range, but actual descent of the greater number is delayed until the coming of severe storms in November. These later severe storms are decisive factors in the fall movement.

In Yosemite National Park, those animals of the upper limits of summer range (9000 ft.) may respond to some undetermined stimuli other than snow and begin their migration in advance of fall storms. The large part of the deer population in the heart of summer range (7500 ft.) shows no great inclination to travel until snow storms occur (p. 25). Even here, the migration is not a positive descent but rather an indefinite movement which tends to carry the animals to areas of little snow. Here, many will linger until heavy snows cause them to descend with a rush to true winter range (p. 27).

In both Yosemite and Yellowstone, severe snow storms are decisive in causing the deer wholly to desert their summer range.

DEPTH OF SNOW

Snow is commonly present on the Yellowstone winter range to a depth of five to fifteen inches. The animals of that region regularly contend with this snow cover from November to March. Much of the Yosemite winter range is below the snow line, and the higher sections of it seldom are covered to a depth of more than five inches (Figs. 4, 5). One or two inches is the usual snow cover here, and there are numerous areas where this small amount of snow melts nearly as fast as it falls. The usual period of snow is four months, as against five in the Yellowstone country.

In comparing the winter behavior of deer in Yellowstone and Yosemite, the writer emphasizes the fact that the Yellowstone animals are taxed with rigorous winter conditions, while the Yosemite animals enjoy comparatively mild weather. Depth of snow, unquestionably, affects the choice of winter range by deer in both regions. The Yellowstone animals of the present seem content with conditions that prevail. Only in years of excessive snowfall, such as occurred in 1910-1911, 1916-1917, 1919-1920, 1921-1922 (Fletcher, 1928) do the deer make a considerable effort to leave the protecting limits of the park. Grinnell and Storer (1924) state that deer cannot feed in snow of greater depth than eighteen inches. In the years mentioned, twenty-four to thirty-six inches of snow covered the normal winter range of the Yellowstone deer. On these occasions, both elk and deer attempted to travel from the park to the lower areas along the Yellowstone River (the winter range of primitive times) and were slaughtered by hunters or died in great numbers from starvation (Rush, 1929, 1930). The ever impending danger of disastrous loss from the causes described has led to national interest in the Yellowstone game herds, and a splendid start has been made in acquiring control of lands north of the park boundary in order that winter range may be extended when severe winters demand it.

In Yosemite National Park, the winter range situation is quite as deserving of study as is the Yellowstone problem. The most cursory examination of the accompanying map (Fig. 3) shows that the park affords all-year protection for no more than five per cent of the deer which in summer reside within the park. Present conditions constitute no great menace (p. 30), but it is impossible to offer assurance that the future may not hold a situation which will constitute a catastrophe for the deer herds. In 1930, a beginning was made by extending the western boundary of the park. 7,725.19 acres, valued at \$3,300,000 were added in the vicinity of Ackerson Meadow, Tuolumne Grove, and the Merced Grove (Albright, 1930).

RELATION OF WEATHER PHENOMENA TO FOOD SUPPLY

In both Yellowstone and Yosemite, the summer diet of deer is characterized by an abundance of succulent herbage with a proportion of woody matter,

such as twigs, bark, and roots, which by bulk may constitute a fifth to a third of the whole. Contents of the few stomachs examined (three in Yellowstone; five in Yosemite) indicate no marked difference in the general nature of summer food for the two regions.

Consistent with the great difference in winter weather conditions for the two localities is the general tendency for the nature of winter food to differ. In Yellowstone, stomachs of deer killed in winter commonly contain eighty per cent or more of woody material, and the remainder is made up of dried grasses and leaves. Most of the Yosemite animals (19 stomachs examined), even in winter, succeed in securing some fifty per cent of their food, by bulk, in green succulent or semi-dried form.

These differences result from the fact that most of the Yosemite winter range lies within a belt in which mild winter conditions permit of continued physiological activity in many plants. Grasses and many other herbaceous plants of the lower Yosemite country are green throughout the winter. At this time, the deer of that region partake of a far greater percentage of grass than is ordinarily recorded by most observers. In contrast with this are the severe winter conditions of all of the Yellowstone region, which bring about complete autumnal changes in forage plants. Yet, deer partake of the woody parts of plants and dried vegetation and, with artificial feeding of hay to supplement this forage, suffer no great loss in ordinary winters (Haberlandt, 1915).

In brief, it is to be concluded that low temperatures, while bringing about a great physical change in forage plants, do not render them unfit for food. Deer could safely reside in winter at high levels in the mountains so far as concerns the food value of high mountain plants. Low temperatures, then, are not the determining factor in fall deer migration.

Deep snow, while it in no way affects the food value of the plants themselves, does effectively render them inaccessible to deer. In this role, it becomes, preëminently, the causative factor in bringing about the fall movement of deer (pp. 11, 27). The spring movement hinges upon two factors in weather phenomena: temperature and snow depth (pp. 16, 31). Although dead plants of the summer range may in the spring become accessible because of the melting of the snow, upward movement of deer does not keep pace with the disappearing snow. The true spring migration awaits the development of new plant growth, and this development is correlated with moderation of temperatures.

HABIT AS A FACTOR IN MIGRATION

Fawns accompany their mothers in making their first migration from summer to winter range. In many instances, too, the young accompany the does in the succeeding journey from winter to summer range. Thus, the

habit of following certain routes of travel, as well as the habit of moving from one range to another, may be founded in individual animals.

Some evidence is found that development of forage controls the spring use of certain migration routes (p. 16), but because deer of a winter locality which is served by more than one route of travel divide in the spring and make use of all routes regardless of development of forage, it is concluded that habit is an important determinant in the choice of migration lanes. In the Sierras, regular use of routes within single drainage systems has served to restrict deer to ancestral summer and winter homes.

Observations made in Yellowstone and Yosemite upon individual deer with natural characters which permit of their identification have provided data upon routes followed (pp. 17, 32). These studies over a period of years reveal that the individual animals habitually follow the same routes of travel. In the Upper Yellowstone-Thorofare region, deer are known to cross the Absarokas, a major divide, in moving from winter to summer range, and vice versa. This instance of failure to follow a single drainage system when migrating indicates that repetition of unusual movements may establish migration habits of an irregular nature.

POSSIBLE INFLUENCE OF SEASONAL PHYSIOLOGICAL RHYTHM

There is a well-marked and nicely correlated seasonal rhythm of breeding, rearing of young, and migration in the mule deer. Feeding habits and migration are closely related to the prevailing environmental complex, and the seasonal movements are controlled by environmental factors. However, the fall restlessness frequently manifested by deer of the Yosemite high country in advance of marked climatological changes seems to indicate a lack of physiological balance and suggests the possibility that a seasonal physiological rhythm may be the underlying cause of the migration. Such a relationship perhaps is the basis of the migration phenomena, but the time of seasonal movements is evidently controlled by environmental factors.

SUMMARY

1. The mule deer of the Yellowstone and Yosemite regions occupy distinct summer and winter ranges. In the spring, they move from the winter range to the higher summer range. In the fall, they reverse this movement. Routes followed are from ten to sixty miles in length.

2. Mating behavior and the birth of young are correlated with the seasonal migration, but apparently no causative relationship exists between these life activities and the migration phenomena.

3. Drops in temperature and early fall snow storms are coincident with a restlessness among deer of the upper summer range, and the fall movement begins with the descent of these animals from the higher levels. Daily mean

temperatures at the time of migration vary from year to year. Mean temperatures of the Yellowstone region are 10° to 20° F. lower than those of similar levels in the Sierras during the migration period.

4. Heavy snow storms are the decisive factor in the fall migration of deer in all parts of the summer range.

5. Dates of snow disappearance control the spring migration only so far as the melting of snow is related to temperatures conducive to plant growth. The spring migration may be delayed for weeks after snow has disappeared from the summer range. Development of forage plants is dependent upon temperature, and the time of spring migration is dependent upon forage conditions.

6. If suitable food is available in a given area throughout the year, some or all of the deer of that area may not migrate. If desirable food becomes limited or inaccessible at some seasons, migrations result and these take the animals to other areas offering an adequate food supply. Availability of desirable food is the most important controlling factor in determining range to be occupied by deer at all times.

7. Evidence suggests that habit is most important in determining the exact migration route followed.

8. A seasonal physiological rhythm may possibly be the underlying cause of the seasonal movements, but availability of food evidently controls the time of migration.

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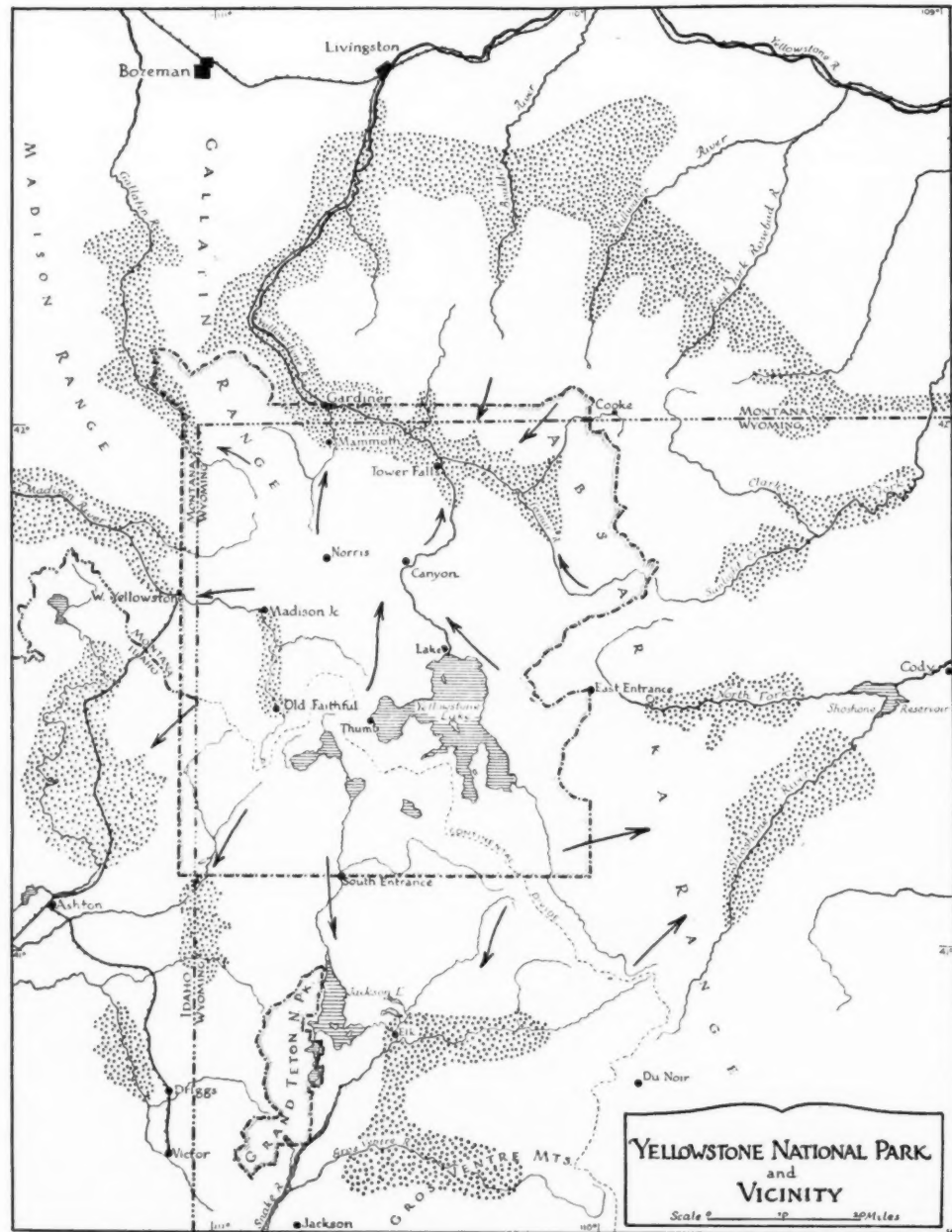
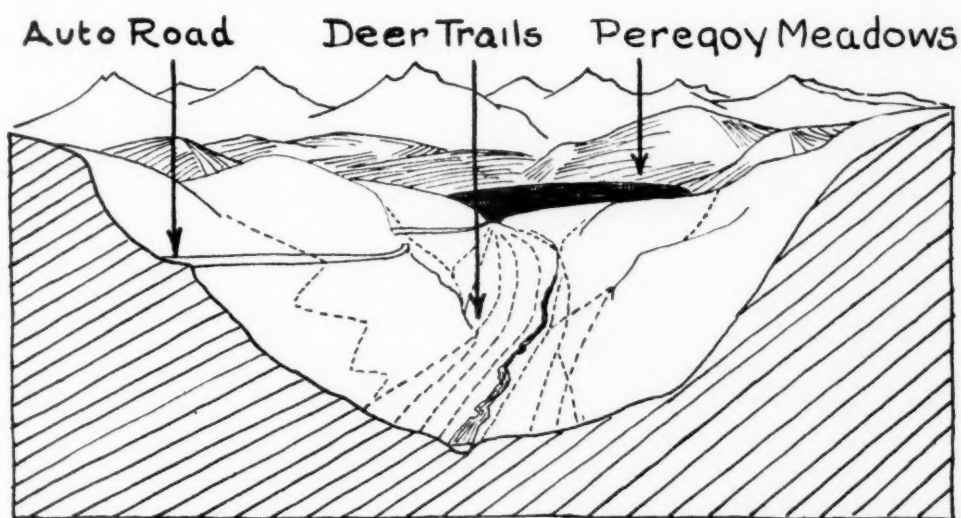


FIG. 1. Winter Range of Mule Deer of the Yellowstone Park Region.

In general, migration routes follow drainage systems. An interesting exception is found in the Upper Yellowstone country, where deer move out of the Yellowstone Valley, cross the Absarokas, and descend to winter range on the Shoshone River.

By far the greater number of deer that occupy the Yellowstone Park plateau (7800 ft.) in summer descend to regions below 7000 feet in winter. Many descend to 5000 feet altitude. Certain deer are known to spend the summer near Thumb (7800 ft.) and the winter at Mammoth (6200 ft.). The route between these two ranges is some sixty miles long. The deer of the Old Faithful-Madison Junction area (7500 ft.) occupy the same range winter and summer. These examples of non-migrants provide an interesting control on the observations and conclusions upon which a part of this paper is based.

MANY PARALLEL TRAILS IN A CANYON USED BY MIGRATING DEER



INDIAN CREEK CANYON

FIG 2. During the course of a movement of deer in the Yosemite region, certain canyons are noted migration routes. In such canyons, parallel trails are numerous, and the general appearance of the canyon floor suggests the presence of great numbers of deer. This "used" appearance is obliterated in the fall by snowfall. The spring movement again leaves its marks upon the canyon, but these evidences are soon wiped out by rains and the growth of plants. Perhaps, but one trail will be conspicuous through the summer. This single trail is used by the comparatively small number of animals that are the summer occupants of the immediate locality.

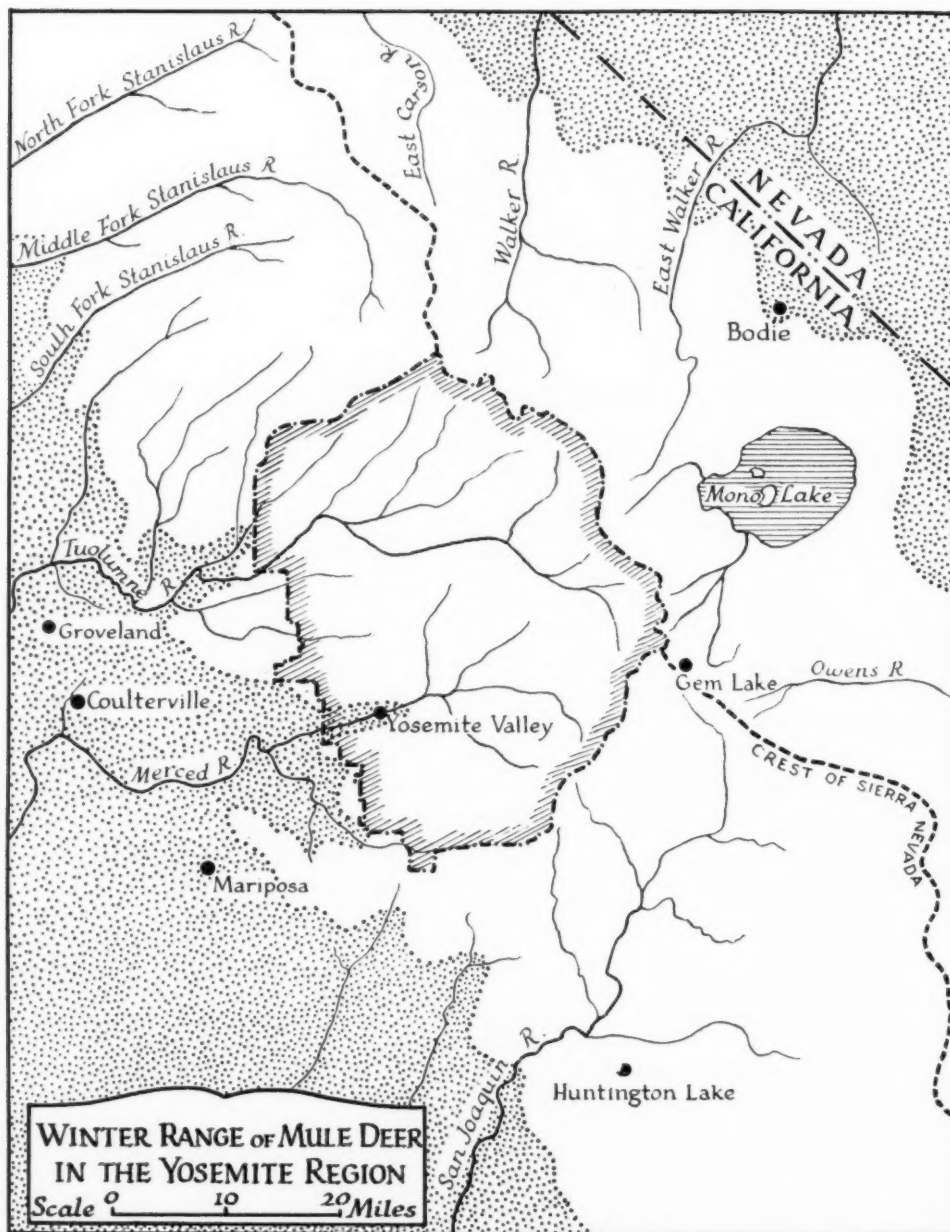
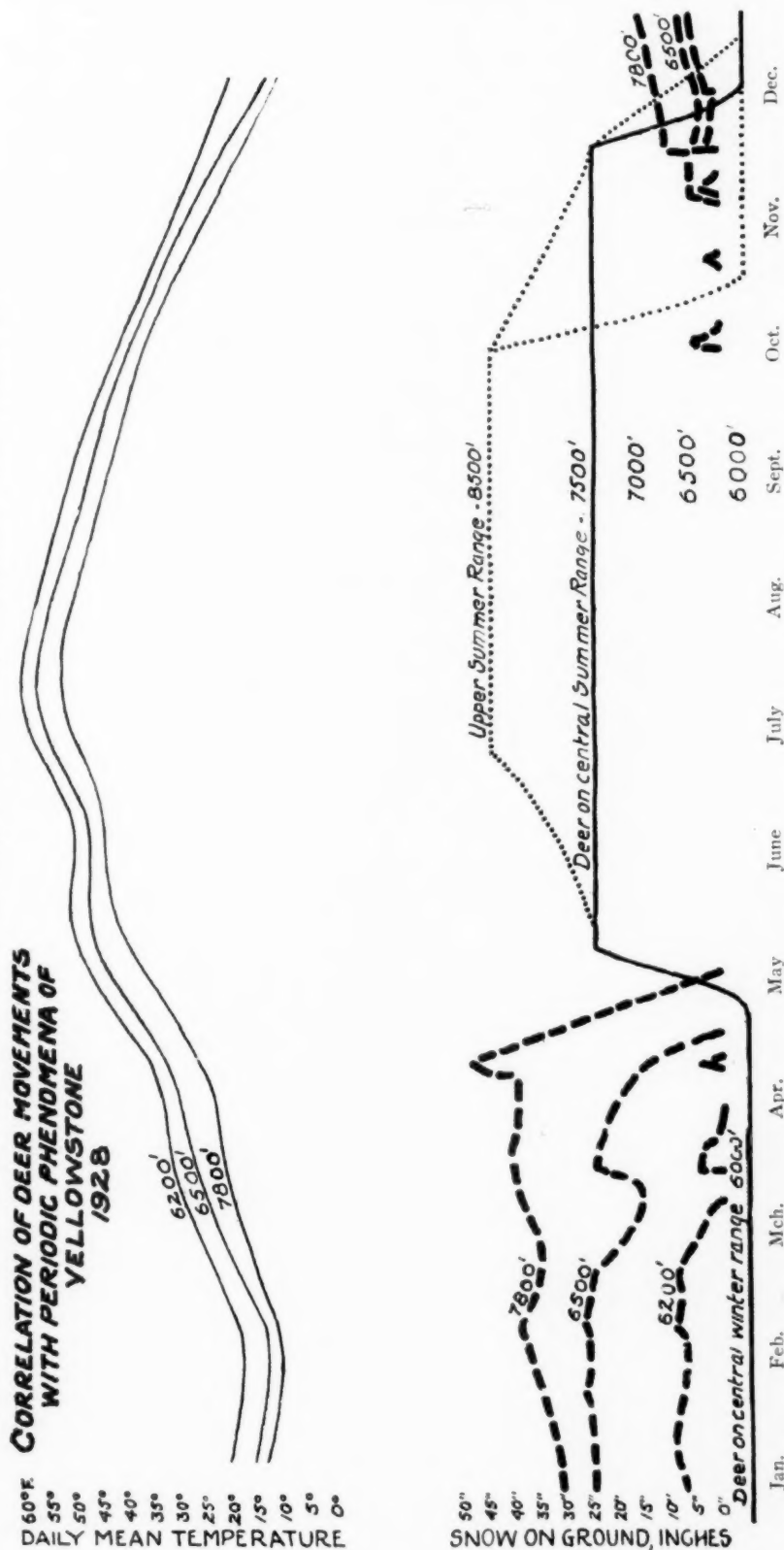


FIG. 3. Winter Range of Mule Deer in the Yosemite Region.

The deer which in summer densely populate the Yosemite National Park are caused to move out of the park when snow falls. They move from their summer haunts (6500 ft. to 9000 ft.) along the stream courses of the west slope of the Sierras to the regions of mild climate in the chaparral and yellow pine belts of 1500 feet to 5000 feet altitude. Immediately east of Yosemite National Park, mule deer live under conditions that differ widely from the situations of the west slope. The animals of the east slope winter in areas 7000 feet to 8000 feet above sea level and experience conditions to be compared with the severe winters of the Yellowstone Park country. Deer of both slopes parallel stream courses when making their seasonal movements and tend to remain in the same drainage systems throughout their lives.

Fig. 4. Deer Movements and Climatological Phenomena; Yellowstone National Park, 1928.



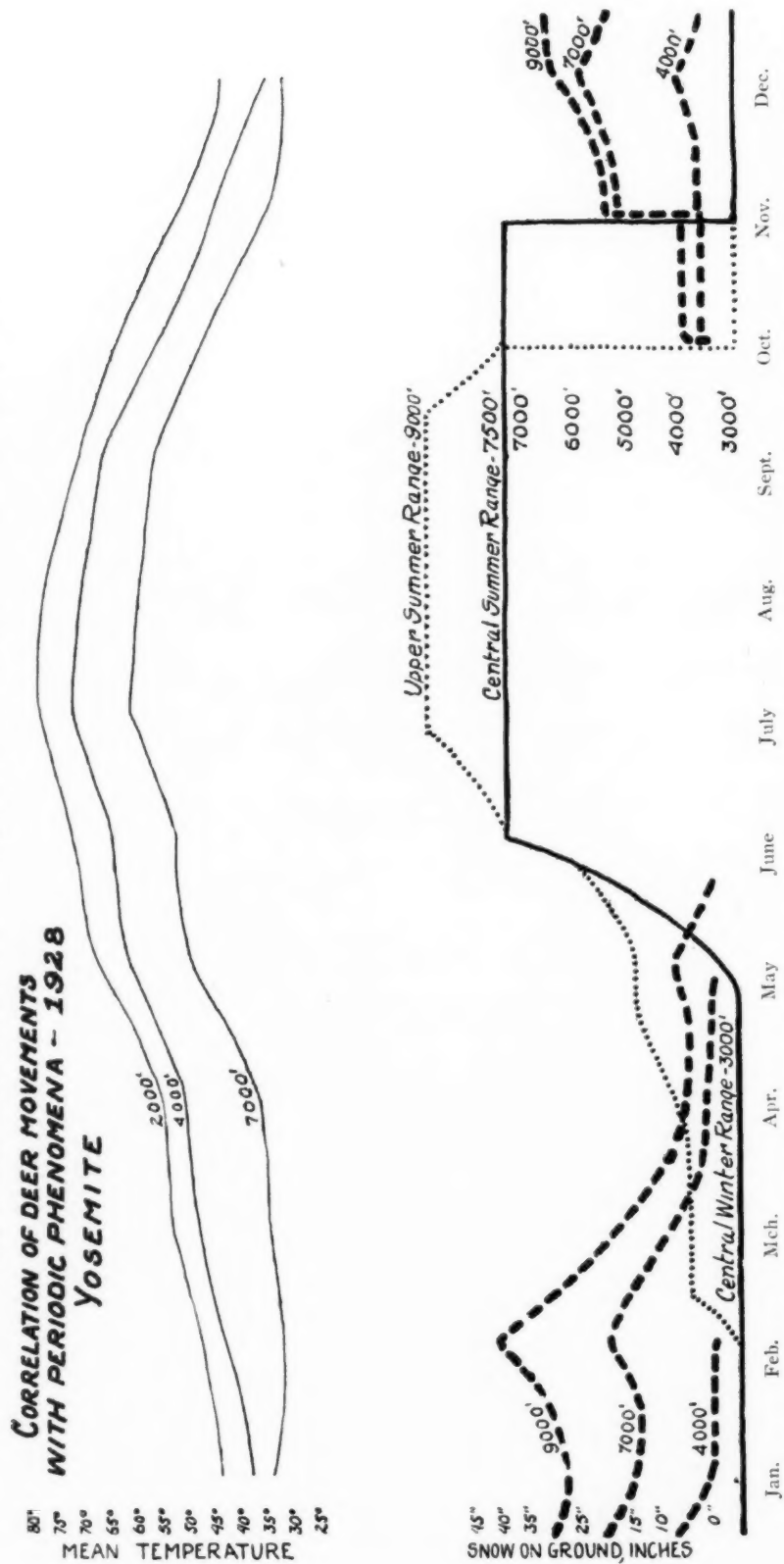
Climatological observations were recorded at Mammoth Hot Springs (6200 ft.), Buffalo Ranch (6500 ft.), and Lake (7800 ft.). Data supplied by the Yellowstone Park Office of the U. S. Weather Bureau.

The deer movements are indicated by solid and dotted lines. The solid line shows altitudinal location of the majority of the animals. The dotted line indicates the movements of a minor number. Snow depth is represented by the heavy broken line.

The snow of the central winter range (6000 ft.) disappeared on April 10. The deer made no movement away from winter range for twenty-two days after the snow was clear. The ascent then (May 5) was steady, and ten days later (May 15) the greater number of the animals were upon the central plateau. The snow line, at this time, was at about the 7800 foot level. The deer remained on summer range for six and one-half months. A snow storm on October 10 started the downward drift of some of those at the upper limits of summer range (8500 ft.). The great majority, however, remained on summer range until the severe snow storm on November 29. Many of these animals were fifty or sixty miles distant from and 1500 feet or 2000 feet above winter range. The journey to winter range frequently took a week or ten days to accomplish.

Analysis: Yellowstone deer do not follow the retreating snow line in the spring. The upward drift is delayed three weeks or a month after snow disappears from winter range. During this time, spring progresses up the mountainsides, and by the time true spring migration is under way, forage plants of summer range have attained the spring condition. The fall movement was initiated by a snow storm, and the decisive stimulus which took all deer to winter range was a severe snow storm.

FIG. 5. Deer Movements and Climatological Phenomena; Yosemite National Park, 1928.



Climatological observations were recorded at Sonora (2000 ft.), Yosemite Valley (4000 ft.), Huntington Lake (7000 ft.), and Gem Lake (9000 ft.). See map.

The deer movement is indicated by solid and dotted lines. The solid line shows altitudinal location of the majority of the animals. The dotted line indicates the movements of a minor number. Snow depth is represented by the heavy broken line.

The movements of a minor number. Snow depth is represented by the heavy broken line. Snow disappeared at the 4000 foot level on February 15. Deer immediately moved up with the retreating snow line. No ascent above the 6000 foot level was made prior to June 7. The 7000 foot level was free of snow (except for drifts or shaded patches) on May 13. It was not until a month later (June 16) that this level was occupied by deer. During the interim, vegetation of that level (7000 ft.) attained the spring state. Most of the snow disappeared on the 9000 foot level on June 5. Deer did not attain those heights until July 13. This year the animals remained on summer range for about five months. The earliest downward drift occurred among the comparatively small number in the upper limits of summer range (9000 ft.). Here, the fall drift preceded snow storms by two weeks. On October 11 several inches of snow fell upon all of the summer range. A decided migration took place during this storm, and many animals arrived on winter range at this time. A greater number, however, remained at 7000 feet in spite of the inch or two of snow, and it was not until the heavy snow of November 10 (18 in. at 7000 ft.) that all of the deer hurriedly left the summer range and occupied true winter range.

Analysis of these data points to the fact that the spring migration up to 6000 feet was controlled by the melting of the snow cover. Above 6000 feet, the movement was delayed about thirty days after the disappearance of snow, during which delay forage plants up to the 7500 foot level attained the spring state. The fall movement of deer in the upper limits of summer range (9000 ft.) began without the impetus of snow storms. In the regions of summer range in which deer were present in greatest numbers (about 7500 ft.), the migration was initiated by snow storms.

THE ECOLOGICAL DISTRIBUTION OF THE MAMMALS
ON THE NORTH SLOPE OF THE UINTA
MOUNTAINS

By

RUTH DOWELL SVIHLA

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THE ECOLOGICAL DISTRIBUTION OF THE MAMMALS ON THE NORTH SLOPE OF THE UINTA MOUNTAINS

INTRODUCTION

In ecology as in taxonomy, there is always a tendency to overdo classification—to attempt to reduce a subject, primarily plastic, to a system of pigeon-hole order. In the field of taxonomy the present tendency is to regard the whole system of classification as constantly evolving and developing in contrast to the older viewpoint of classification as a fixed and rigid system. Systematists are realizing that classification is merely the means to an end and must be kept as plastic as Nature herself. So with the study of an ecological subject, the schemes of classifying the data secured must be flexible to accommodate plastic material.

The community of interest of plant and animal ecologists is becoming more and more recognized. After all, plants and animals are both fundamentally protoplasm and while the details of their reactions and responses differ, the principles involved are the same. Plant ecology has advanced far beyond its sister field of animal ecology. It then behooves the animal ecologist to study well the methods and results of this related field in order to gain the advantages of its advances and to avoid its errors. Methods and concepts which have become more or less recognized in plant ecology should be scrutinized well as to their adaptability for animals. There is, perhaps, a human tendency to run to extremes—either to accept concepts with enthusiastic optimism or else to discard them entirely. It is to be hoped that in such a comparatively new field as animal ecology, a conservative course will be pursued, that methods and concepts will be tested critically and impartially before they are accepted or rejected and that where it becomes obviously necessary old ones will be modified or new ones evolved.

So far surprisingly little has been done in the way of actual field study of the ecological distribution of mammals as a group. Such workers as Grinnell and Swarth (1913), Shelford (1913), Grinnell (1914), Dice (1916), Grinnell and Storer (1924), Elton (1927), Merriam (1898) and his co-workers, and others have considered mammals in connection with the distributions of other vertebrates and invertebrates to varying extents. Aside from numerous annotated lists and descriptions of mammals and their habitats (Harper, 1929; Harper and Harper, 1929, and others) Adams (1908) is, perhaps, the only worker who has considered mammals by themselves to any extent in relation to ecological concepts.

In the present study, only the mammals were considered inasmuch as the distributions and ecological relationships of one group of animals are not necessarily the same as those of another. In an attempt to untangle the in-

terrelationships of animals and their environments, it seems most expedient to simplify a complicated matter as much as possible by considering the problems of one group of animals at a time.

The purpose of the present study has been fourfold: (1) to secure actual field data concerning the ecological distributions of the mammals on the north slope of the Uinta Mountains; (2) to classify these data flexibly according to different schemes of distributional classification; (3) to determine, by comparing the average indices of restriction for these different groupings, the most applicable scheme of classifying the distribution of the mammals of this region; and (4) to evaluate certain more or less accepted concepts according to the data secured.

The region chosen covers a comparatively small but diversified area. The inclusion of two topographic zones, four vegetation belts, various habitats and some 6000 feet of altitude made the study of both distributional and ecological problems possible.

Two summers (1928 and 1929) were spent in the field securing data. Notes and field observations on the habits, distributions and habitat relationships of the mammals were made. A total of 609 specimens were collected. The majority of these are now in the collections of the Division of Mammals, Museum of Zoology, University of Michigan. These represent 35 species and subspecies. The presence and distribution of eleven others were determined by means of tracks, pellets, authentic reports or personal observation. A large series of *Peromyscus maniculattus osgoodi* (263 specimens) was secured besides 33 live specimens which were sent to the Museum of Zoology, University of Michigan, as a breeding stock for variation studies carried on by Dr. L. R. Dice. An annotated list of the mammals of the Uinta Region, including the number of specimens taken and notes on their ecological distributions, has been published elsewhere.¹

Plants (74 species) which formed the dominant vegetation of the various zones, belts and habitats, were collected as well as species which were used as food by the mammals. These are preserved in the Herbarium of the University of Michigan. Identification of the plant material was made by Lois S. Ehlers, Dr. J. H. Ehlers, and Clair Brown. I am indebted to the Museum of Zoology of the University of Michigan for opportunity and facilities for carrying on this study; to Dr. L. R. Dice for constant help and advice throughout the work; to Prof. H. H. Bartlett who with characteristic generosity has given his valuable time and untiring patience; to Arthur Svihla for unfailing help in the field; and to the residents of the Uinta Mountain Region, who have proven the cordial hospitality of the West. The William P. Harris Jr. Research Fund has aided materially in helping to support the field work in this study.

¹ Jour. Mammal. 12: 256-266.

THE UINTA MOUNTAINS

LOCATION AND TOPOGRAPHY

The Uinta Mountains lie in the northeastern corner of Utah close to the Wyoming line and run in an east-west direction at practically the same latitude as Salt Lake City. They are a branch of the Wasatch Mountains (Powell, 1875) which lie at the west and extend in a north-south direction. These two ranges are at right angles to each other and are separated by the valleys of the Provo and Weber Rivers (Atwood, 1909), a distance of not more than ten miles (Fig. 1). The Uinta Mountains form an elongated, flat-topped arch (Boutwell, 1903) relieved by several high peaks. They are approximately 150 miles long and 35 miles wide. The main east-west divide lies north of the center of the range so that the northern slope is considerably steeper than the southern. The altitude of the range varies from 6500 feet to peaks more than 13,000 feet high (Boutwell, 1903).

The region considered in this study consists of a transect running from the sagebrush plains of the southwestern part of Sweetwater County, Wyoming and the adjacent portions of Daggett County, Utah, up the north slope of the Uinta Mountains somewhat east of the midpoint of the range (Figs. 2, 3). The mountainous part of the region lies within the boundaries of the Ashley National Forest. In altitude this transect ranges from 6000 feet, the valley of Henry's Fork, to 11,900 feet, the top of the peak known locally as the Nipple. This covers approximately thirty miles by road and trail or twenty miles in a straight line.

CLIMATE

Information concerning the climate of this region has been compiled from climatological data sheets and maps of the United States Weather Bureau (Day, 1920). The data (Table I) are those for Manila, Utah, which is the only station maintained in this region on the northern side of the mountains. Manila has an elevation of 6225 feet and is situated in the Lucerne Valley which lies in the sagebrush belt according to the classification used in this study. Hence, these data apply to a rather arid part of the region considered. Manila falls within the general range of 10 to 15 inches of mean annual precipitation. The belts of increasing amounts of precipitation up the mountain approximate in a general way the belts characterized by yellow and lodgepole pine (15 to 20 inches); spruce and fir, and alpine vegetation (more than 20 inches). On the southern slope of the mountains at an elevation of 5266 feet, lies Vernal, the climate of which is interesting by way of comparison. The precipitation data are different as would be expected. At Manila the greatest amount of rainfall occurs in the spring (April, 1.65 inches). The annual mean is 10.09 inches. At Vernal the greatest mean precipitation occurs in September with 1.2 inches and the annual mean is 8.67

inches. Although the mean annual temperatures of the two places are only slightly different (41.8° F. at Manila and 45.8° F. at Vernal), the frost data are such that the average length of the frostless season at Manila is 78 days while at Vernal it is 127 days. The effect of such a difference in length of growing season is seen in the fact that the Vernal region produces by far the greater amount of fruits and vegetables.

DISTRIBUTIONAL CLASSIFICATION OF THE MAMMALS OF THE UINTA REGION

TOPOGRAPHIC ZONES AND FAUNAE

The Uinta Region may be divided into two great topographic zones, the Plains Zone and the Mountain Slope Zone (Fig. 3). The Plains Zone includes the Sagebrush Vegetation Belt and is contingent with it. This zone is characterized by more or less rolling sagebrush plains subjected to relatively high summer temperatures, low winter temperatures and an annual rainfall averaging approximately 5 to 10 inches. In contrast to this, is the cool moist mountain slope extending from 8000 feet in altitude up to approximately 12,000 feet. This includes the three vegetation belts: Pine, Spruce and Fir, and Alpine.

Each of these two zones is distinguished by a number of characteristic species of mammals. However, there are in addition to these, 21 species which are common to the two zones, thus showing a distinct zonal overlapping. Fig. 3 shows that 13 species occur in the Plains Zone only, 21 species (including the bison) in both the Plains and Mountain Slope Zones, and 10 species in the Mountain Slope Zone only.

VEGETATION BELTS AND FAUNAE

This region falls naturally into four great belts of vegetation, namely: the Sagebrush; the Yellow Pine and Lodgepole Pine; the Spruce and Fir; and the Alpine (Figs. 2, 3). These belts are more or less sharply defined although there is considerable interdigitating and overlapping in places. This occurs especially in the mountain parks and along the streams and canyons. Between the Sagebrush and Pine Belts there is a minor cedar-pinyon area. This forms a fairly well marked belt on the southern slope of the mountains but is not extensive or as definite on the northern slope. It is confined to the arid slopes of the foothills, has no characteristic mammals and so is considered here as a minor belt. The vegetation belts range in altitude from 6000 feet, the sagebrush plains, to 12,000 feet, the top of the Nipple. The average annual rainfall increases with the altitude so that although 10 to 15 inches fall on the sagebrush plains, considerably more than 20 inches is the average annual precipitation on the mountain top (U. S. Weather Bureau, Chart I).

The mammal faunae of the vegetation belts are shown in Table III. The

Sagebrush Belt is the only one that has any significant number of characteristic mammals. Each of the other belts has but one species at most which is found only within its limits. However, grouping the three upper belts together, there are 10 species of mammals which occur only within their limits; compared with 13 which occur only in the Sagebrush Belt. There are, nevertheless, 21 species which are found in both the Sagebrush and upper belts. This lack of zonation in the distribution of the mammals is discussed later (p. 65).

SAGEBRUSH BELT AND FAUNA

Sagebrush, *Artemisia tridentata* Nutt., is the dominant plant over the broad general area which extends from the plains region of southwestern Sweetwater County, Wyoming, across the Lucerne Valley of northeastern Daggett County, Utah, to the foothills of the Uinta Mountains (Fig. 4). This belt ranges from 6000 feet to approximately 8000 feet in altitude and coincides practically with the region which has 10 to 15 inches of average annual rainfall. The upper portions of this belt include the cedar-pinyon area which occupies the more exposed parts of the foothills and the rocky slopes. Sagebrush forms the undergrowth of the sparse and scattered stands of cedars, *Juniperus utahensis* Engelm., and pinyons, *Pinus edulis* Engelm., and extends up to 9000 feet into the Pine Belt where it is restricted to the mountain parks (Fig. 9). Such an extension of a typical plains belt up into the forest belt carries with it characteristic habitats so that often a mixture of mammal species results. The Sagebrush Belt includes the following habitats: Sagebrush, which is the dominant habitat; Rock Cliff; and Streamside.

The total mammal fauna of this belt (Table III) includes 32 species. Thirteen of these are found only in this belt. The remainder are ranging forms which occur also in the upper belts.

BELT AND FAUNA OF YELLOW PINE AND LODGEPOLE PINE

The Pine Belt ranges from approximately 8000 feet in altitude to 10,500 feet and has an average annual rainfall of 15 to 20 inches. Here on the northern slope, yellow pine, *Pinus ponderosa* Dougl., and lodgepole pine, *Pinus murrayana* Balf., intermingle to form one general belt of vegetation in which yellow pine is more in evidence at the lower altitudes. The lodgepole pine supersedes the yellow pine over burned areas and in places occurs up into the spruce-fir forest. It forms such dense stands (Fig. 9) that practically no undergrowth can survive the subdued light conditions. This is in direct contrast to the open yellow pine forest (Fig. 13) which supports an extensive undergrowth of sagebrush, grasses and flowering plants. Mountain parks are relatively abundant in this belt. They consist of sagebrush interspersed with grasses. Along the canyons (Fig. 8), Douglas firs, *Pseudotsuga mucronata* (Raf.) Sudw., and aspens, *Populus aurea* Tides., occur

and often reach down into the Sagebrush Belt, thus extending the ranges of some of the forest mammals into an otherwise plains belt. Aspens also occur along the edges of the parks, where moisture conditions are favorable. This belt includes the following habitats: Forest, which is the dominant habitat; Rock Slide; and Streamside.

Of the 28 species of mammals which range into or through this belt, only one (*Zapus princeps princeps*; Table III) is restricted to it.

SPRUCE-FIR BELT AND FAUNA

This is relatively a narrow belt on the northern mountain slope extending (Fig. 15) from approximately 10,500 feet in altitude to timberline at 11,700 feet. Engelmann spruce, *Picea engelmanni* Parry, is the dominant tree and the subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., is subdominant. Occasionally one also finds a Colorado spruce, *Picea pungens* Engelm. As a whole, this belt is open and supports an undergrowth of herbaceous plants, chief among which is the grouse whortleberry, *Vaccinium scoparium* Leiberg. Occasionally there are small boggy areas supporting a growth of sedges. The rainfall in this belt averages over 20 inches per year but the growing season is considerably shorter than that of the lower belts. The following habitats are recognizable: Forest, which is dominant; Rock Slide; and Streamside.

Twenty-three species of mammals are found in this belt, but only one, *Clethrionomys gapperi galei* (Table III), is restricted to it.

ALPINE BELT AND FAUNA

The Alpine Belt includes timberline and above. Hence, in the Uinta Region, it ranges from 11,700 feet to approximately 12,000 feet in altitude. Except for the very narrow line of krumholz and interspersed mountain meadows, it is nothing but a huge rock slide made up of pre-Cambrian red sandstone (Fig. 16). The krumholz consists of dwarfed and stunted Engelmann spruce and scattered patches of alpine willow, *Salix wolffi* Bebb. The meadows support a rich although dwarfed flora of grasses and flowering plants. Rainfall here is more than 20 inches per annum but on account of the steepness of the slopes and shallowness of the soil, most of it runs off and so is but slightly available to plant life. The growing season is less than two months in length and frosts may occur at any time during the summer. The habitats are Rock Slide, which is dominant, and Alpine Vegetation.

Of the 10 species of mammals which range through this belt, only one, *Thomomys*, sp. (Table III), can be considered peculiar to it.

HABITATS AND COMMUNITIES²

The following types of habitats are recognizable in the Uinta Region: Sagebrush; Streamside; Rock Cliff; Rock Slide; Forest; and Alpine Vegetation.

² For the senses in which these terms are used see p. 64.

tion. Some of these habitats are confined to one vegetation belt, as, for example, the Rock Cliff and the Alpine Vegetation Habitats. Others may occur in several belts, as, for instance, the Streamside, Sagebrush, and Forest Habitats. Each habitat shelters a community of mammals which may vary as the habitat becomes modified but as the term is used in this paper (p. 64), must contain one or more species peculiar to it in order to be significant in determining mammal distribution in the region. Many of these habitats may be subdivided into subhabitats or unit habitats but this has been done only when a mammal is obviously restricted to a certain modified area within a habitat. Table III shows the habitat-types and their respective mammal communities.

SAGEBRUSH HABITAT AND COMMUNITY

The Sagebrush Habitat shelters the Sagebrush Community of mammals and forms by far the greater part of the Sagebrush Belt in which it is the dominant habitat (Fig. 4). With the exclusion of the Streamside and Rock Cliff Habitats of the Sagebrush Belt, this habitat covers the rest of the belt. It extends up through the minor belt of cedar-pinyons into the Pine Belt where it forms the greater part of the mountain parks. Sagebrush, *Artemisia tridentata* Nutt., is the dominant plant of this habitat. On the plains north of Henry's Fork local areas of mat saltbush, *Atriplex corrugata* Ryd.; gray molly, *Kochia vestita* (S. Wats.) Ryd.; and two species of cacti occur. In some places there are areas of very sandy soil which are designated as subhabitats of the kangaroo rats, *Dipodomys* sp., for it is only here that they are found. Greasewood, *Sarcobatus vermiculatus* (Hook.) Torr., and rabbit brush, *Chrysothamnus graveolens* (Nutt.) Greene, are local in range along the banks of old stream beds. On the slopes of the foothills in the cedar-pinyon area and in the mountain parks of the Pine Belt, the Sagebrush Habitat becomes subdominant. Here, June grass, *Koeleria cristata* (L.) Pers., grows interspersed with the sagebrush. This grass is very luxuriant in early summer and provides one of the best forage plants for livestock grazing. The deer mouse and the jack rabbit extend their ranges up into the mountain parks of the Pine Belt along with the sagebrush. Above approximately 9000 feet in altitude, sagebrush gives way to shrubby cinquefoil, *Potentilla fruticosa* L., in the few mountain parks which occur above this altitude. The deer mouse was not found to occur any higher up the mountain side than where the sagebrush occurred.

Of the 18 species of mammals which were found in this habitat (Table III), 6 are restricted to it.

ROCK CLIFF HABITAT AND COMMUNITY

In contrast to the Rock Slide Habitat of the upper belts, which is made up of large blocks of pre-Cambrian sandstone, the Rock Cliff Habitat is found only in the Sagebrush Belt. It is formed from the up-tilted beds of

rocks ranging from Pennsylvanian to Cretaceous in age (Atwood, 1909). Such Rock Cliff Habitats are found just north of Henry's Fork, along Sheep Creek and at Hide Out on Green River. Where the cliffs are high talus slopes are formed at the bases. Cedars, *Juniperus utahensis* (Engelm.) Lemmon, and two species of cacti have become established on many of these slopes (Fig. 7).

The Rock Cliff Habitat shelters a community of mammals, three of which are peculiar to it (Table III). These species, *Peromyscus crinitus auripectus*, *Peromyscus boylei rowleyi*, and *Eutamias dorsalis utahensis*, are all characteristic of the southwestern desert region. The records for the two subspecies of *Peromyscus* are extensions of their known ranges.

STREAMSIDE HABITAT AND COMMUNITY

The Streamside Habitat includes the stream, its banks and adjacent areas which are conspicuously influenced by it. This habitat occurs in the Sagebrush, Pine and Spruce-Fir Belts. The streams in this region usually have their origin in the glacial lakes of the cirque-like basins just below timberline in the Spruce-Fir Belt. They flow with great rapidity down the steep slopes of this belt. In the Pine Belt, which spreads away at a gentler angle, their speed is accordingly reduced. Here they flow through the sagebrush parks and supply the adjacent vegetation with an abundance of water. In places thick stands of willow, *Salix geyeriana* Anderss., which form the willow subhabitat of the jumping mouse, *Zapus princeps princeps*, occur along the banks (Fig. 12). Quite distinct from the sagebrush which makes up the greater part of the parks, is the narrow strip of grass which lines the streams (Fig. 10). This is called the grassy flood plain subhabitat of the pocket gopher, *Thomomys pygmaeus*.

Streams often form canyons down the mountain side and thus extend the flora and fauna of the upper belts into the lower ones. Sheep Creek illustrates this (Figs. 6 and 8). According to the altitude and the adjacent dominant vegetation, this habitat is in the Sagebrush belt, but the presence of upper belt plants and mammals here show that these species have followed the cool streamside from the upper belt down into the Sagebrush Belt. This overlapping of belts results in a mixture where species which are characteristic of the Forest, Streamside, and Sagebrush Habitats intermingle. Douglas fir, *Pseudotsuga mucronata* (Raf.) Sudw., aspen, *Populus aurea* Tides., columbine, *Aquilegia caerulea* James, and Rocky Mountain bee plant, *Cleome serrulata angustata* (Jones) Tides., occur here with such sagebrush species as sagebrush, *Artemisia tridentata* Nutt., and rabbit brush, *Chrysothamnus graveolens* (Nutt.) Greene, and *Chrysothamnus linifolius* Greene; and such streamside species as cottonwood, *Populus angustifolia* James, water birch, *Betula fontinalis* Sarg., and willow, *Salix lasiandra* Benth. The pine squirrel, *Sciurus fremonti fremonti*, and the porcupine, *Erethizon epixanthum epix-*

anthum, range from the Forest Habitat of the upper belts down along this creek. The pocket gopher, *Thomomys pygmaeus*; shrew, *Sorex palustris navigator*; and chipmunk, *Eutamias minimus consobrinus*, are also upper belt species and were found in the Sagebrush Belt only along Sheep Creek.

Sheep Creek is an intergradation area for the *minimus* series of chipmunks. *Eutamias minimus consobrinus* at this locality approaches *Eutamias minimum minimus* in such characters as ear length and color. Typical *consobrinus* is found up the mountain slopes while at Green River City, Wyoming, which is well in the Sagebrush Belt, typical *minimus* occurs. At Henry's Fork, which is in the Sagebrush Belt but also in the foothill region, *minimus* approaches *consobrinus* in ear length and color characters. Thus, there is a gradation from typical *minimus* of the Sagebrush Belt to *minimus* approaching *consobrinus* and *consobrinus* approaching *minimus* in the foothill region to typical *consobrinus* on the mountain slope.

Of the 27 species of mammals found in the Streamside Habitat (Table III), 15 are restricted to it.

ROCK SLIDE HABITAT AND COMMUNITY

The Rock Slide Habitat consists of huge blocks of red sandstone which form slides in the Pine (Fig. 14), Spruce-Fir and Alpine belts. In the latter belt, it is the dominant habitat (Fig. 16). It remains unchanged throughout these belts and shelters a community of 7 mammals. Two of these, the deer-mouse, *Peromyscus maniculatus osgoodi*, and the golden-mantled ground squirrel, *Callospermophilus lateralis lateralis*, are not found further up the mountain than the Pine Belt; one, the wood rat, *Neotoma cinerea orolestes*, no further than the Spruce-Fir Belt; while the other four, the pika, *Ochotona princeps uinta*, hoary marmot, *Marmota flaviventris nosophora*, and two chipmunks, *Eutamias umbrinus* and *Eutamias minimus consobrinus*, extend up into the Alpine Belt (Table III).

FOREST HABITAT

The Forest Habitat consists of the forest areas of the Pine and Spruce-Fir Belts and so becomes the dominant habitat of these belts. In the Pine Belt, this habitat includes dense stands of lodgepole pine and the open growth of yellow pine (Figs. 9, 13). Aspens, Douglas firs, and other moisture requiring trees occur especially along the streams. These often extend down into the Sagebrush Belt and help to form the mixed habitats described on page 56. The yellow pine area supports an undergrowth of sagebrush and such herbaceous plants as bitterroot, *Lewisia rediviva* Pursh.; mountain death camas, *Zyadenus elegans* Pursh.; alum root, *Heuchera parvifolia* Nutt.; stone crop, *Sedum stenopetalum* Pursh.; columbine, *Aquilegia caerulea* James; paint brush, *Castilleja* sp.; sego lily, *Calochortus nuttallii* Torr. and Gray; larkspur, *Delphinium geyeri* Greene; etc. In the upper

parts of the Pine Belt, mountain juniper, *Juniperus sibirica* Burgsd., and bearberry, *Arctostaphylos uva-ursi* (L.) Spreng., occur. In the Spruce-Fir Belt (Fig. 15), besides the characteristic trees which are found here, there is a thick ground cover of grouse whortleberry, *Vaccinium scoparium* Leiberg. This habitat provides both food and shelter for the pine squirrel, *Sciurus fremonti fremonti*, the flying squirrel, *Glaucomys sabrinus bangsi*, and the porcupine, *Erethizon epixanthum epixanthum*, which are the characteristic mammals (Table III).

ALPINE VEGETATION HABITAT

This includes timberline krumholz and alpine meadow. The krumholz is made up of dwarfed Engelmann spruce, *Picea engelmanni* Parry and dwarfed willow, *Salix wolfii* Bebb. The alpine meadows are areas of varying sizes which are interspersed between extensive rock slides and the narrow line of krumholz (Fig. 16). The vegetation is low but very luxuriant during the short growing season. It consists of such plants as saxifrage, *Saxifraga* sp.; daisy, *Erigeron uniflorus* L.; pygmy bitterroot, *Lewisia pygmaea* (Gray) Robins; catch-fly, *Seiophora acaulis* L.; paint brush, *Castilleja* sp.; wood betony, *Pedicularis parryi* Gray; clover, *Trifolium parryi* Gray; knotwood, *Polygonum bistortoides linearifolium* (Wats.) Small; geum, *Sieversia turbinata* (Ryd.) Greene; and the thistle, *Carduus lanceolatus* L. The last two plants are used by the pikas, *Ochotona princeps uinta* (Fig. 17), for food and are stored away in piles during the summer. Deer, *Odocoileus hemionus hemionus*; elk, *Cervus canadensis canadensis*; and formerly bison, *Bison bison bison*, range up into this habitat for summer forage. Chipmunks, *Eutamias umbrinus* and *Eutamias minimus consobrinus*, occur here, as well as hoary marmots, *Marmota flaviventris nosophora*, and pikas, *Ochotona princeps uinta* (Table III). The Uinta pocket gopher, *Thomomys uinta*, is restricted to those meadows where the soil is deep enough to be workable.

SCHEMES FOR CONSIDERING DISTRIBUTION

THOSE IN COMMON USE

The various systems for classifying animal distributions have been discussed by Dice (1916). There are the zoogeographical, the life-zone, and the ecological systems. The life-zone system, exemplified by the life zones of Merriam (1898) and used by him and his co-workers, is based presumably upon temperature as the controlling factor. His life zones may be divided secondarily into faunal areas according to differences in humidity. The ecological viewpoint stresses the relationships which exist between animals and their more immediate environments. Animals are grouped according to similar habitats, communities or associations, all of which refer to the more immediate environmental conditions than do life zones. Shelford and his co-

workers have emphasized this point of view. Shelford (1913) included all animals, both invertebrate and vertebrate, into a classification of community-types based upon similarity of ecological behavior.

There has been a tendency to combine and modify these two viewpoints. Grinnell (1914) discussed both the zonal and the ecological or associational systems. He found that in California there were "three distinct orders of distributional behavior"—zonal, based upon temperature; faunal, based upon humidity; and associational, based upon environmental conditions. He classified the birds and mammals of the region into these three categories. Grinnell and Swarth (1913) used a similar classification. Dice (1916) found that the life zones of Merriam could not be applied consistently to the distributions of the land vertebrates of southeastern Washington. He classified the land vertebrates of this region as occurring in habitats which were grouped into faunal areas indicated by the dominant vegetation. Taylor (1922) grouped the birds, mammals and plants of Mt. Rainier, Washington, into life zones limited by temperature, and habitats with their associations which were based upon water relations. All this schemes are based presumably upon different combinations of the factors, temperature, humidity, vegetation and habitat.

NEED FOR A FLEXIBLE BASIS IN CLASSIFYING DISTRIBUTIONS

The main points in dispute in these classification schemes are the relative importance of the factors involved and their application to different groups of animals. It is only to be expected that different factors will be of different importance for different animals and animal groups. For instance, the kangaroo rat is limited primarily in its distribution by the nature of the soil, whereas the pine squirrel is found only where coniferous trees provide suitable food and shelter. In general, some insects are limited particularly by vegetation while land barriers limit the distributions of fishes. The determining factors will also differ markedly in different regions. Life zones, based upon temperature, may be definite and clear-cut with characteristic species, say, on San Francisco Mountain, but these same life zones with their indicators may not be recognizable or even present in southeastern Washington. Criticisms of the limitations of the life-zone system have been made by Trotter (1912), Shreve (1914), Dice (1916), Ruthven (1920), and others.

The chief difficulty in the application of the life-zone system appears to lie in the fact that temperature, the factor upon which it is presumably based, is not necessarily the critical factor in every region, and hence, this system cannot be applied indiscriminately. It is generally conceded that the distributions of animals, and indeed plants also, are determined rather by a complex of interacting factors than by one factor alone, although one factor may nevertheless be of more immediate influence than the others.

Would it not be far more satisfactory to have a completely flexible basis for classifying animal distributions so as to allow the recognition of the predominant importance in each region of the factor or factors which there, more than any other factor or factors, determine distribution? Thus, in a region where temperature is obviously the predominating factor, temperature zones could be indicated. Where humidity is dominant or where the vegetation or physiography is the conspicuous influence, humidity, vegetation or physiographic zones, belts or areas could be designated. Furthermore, a region may not be divisible into zones or larger divisions based upon the dominance of any one of these factors, but nevertheless might be classified according to habitats or associations which themselves represent organic response to a complex of environmental factors in which no single one necessarily controls. When all of these factors are influential and their effects of such a nature as to be separately discriminated, they all could be used in the order of their relative importance. If, as may very well happen in some regions, all the factors seem to be of equal importance, this should be admitted by the simultaneous recognition of more than one scheme of classification for a single region. One scheme may even be preferred arbitrarily to the others in order to emphasize or illustrate a certain point of view or method of attack. Such terms as zones, belts, areas, habitats and communities which are general and ordinarily used in an unrestricted sense, appear to be far more desirable than such terms as life zones, faunal areas and associations, because these latter terms have come to possess almost as many meanings as there are authors who have used them. General terms are easily modified by adjectives to fit the region under consideration.

The combinations of zonal and ecological methods of classification as used and modified by Grinnell, Grinnell and Swarth, Dice, Taylor and others have approached such a flexible system as proposed here. In their classifications, these authors have recognized the fact that the distributions of animals over a region may be controlled by their relationships to more than one factor by using more than one scheme of classification. For instance, Grinnell (1914) used three schemes of classifying the birds and mammals of California, thus recognizing the influence of three conspicuous factors. In this way he established a relatively flexible basis for classification.

Nichols (1929, pp. 629-641), in discussing the classification of plant associations, has pointed out three totally different viewpoints: (1) inherent composition and structure; (2) geographical relationships; and (3) succession. These have been used by plant ecologists in the interpretation of ecological relationships. "Any one of them, by itself, may be taken as a rational basis for ecological classification." He brings out the fact that in attempting to classify the facts of nature, no automatic or precise system can be devised. Differences in interpretation are inevitable and the "best that any scheme . . .

can hope to do is to furnish a sound framework, based upon generalized facts and fundamental principles." This very sane viewpoint may well be applied to the various schemes of classifying animal distributions.

Cooper (1926, p. 396) has recognized the necessity of classification as a foundation for understanding the various phenomena of plant ecology, but has emphatically warned against the use of a rigid, pigeon-hole system in which to cram the "fluent" processes of nature. Again (p. 412) he urges "fluency in the treatment of fluent material" and the "abandonment of concepts and terms which clearly tend toward rigidity."

AN INDEX OF RESTRICTION

In this study, only one group of animals, the mammals, is considered. The reason for this is obvious. The distribution of one group of animals over a region is not necessarily the same as that of another group over the same region. Hence, a classification is not necessarily applicable to more than one group. For instance, what may be a unit habitat for a number of mammals may include a dozen or more types of habitats or their equivalents for insects. The forest type of habitat for mammals considered in the Uinta Region, if applied to insects, would, no doubt, be subdivided into areas including different species of trees, each of which would be further divided according to strata. The streamside type of habitat, as it is considered in this region, shelters one definite type of mammal community, but if the bird distributions were considered, it would become necessary to divide it into several habitats including open water, shoreline, and brushwood.

A flexible system of classification, such as is described, is used in this paper. The aim has been to classify the mammals of the region in the most natural way possible according to what appear to be the conspicuous factors in their distributions. From data secured in the field, the mammals were grouped according to habitat-types, vegetation belts and topographic zones, for as viewed in the field, these were obviously the natural groupings. It was found that by comparing the proportion of restricted species to that of wide ranging species for these different classifications, that an index of the relative degree of restriction is obtained. By comparing the averages of these indices, the relative degree of restriction of the different groupings is revealed—the higher averages of course showing the greatest evidence of mammal restriction. It was found that the immediate environmental conditions or the habitat show the greatest degree of restriction and so form the most logical basis for classifying the mammal distributions in this region.

The relative degree of habitat restriction of mammal communities may be expressed by the proportion of restricted species to that of wide ranging species. This is illustrated by the following tabulation:

Type of habitat	Restricted species (<i>R</i>)	Wide ranging species (<i>R'</i>)	Index of restriction $\left(\frac{R}{R + R'}\right)$
Streamside	15	12	55
Rock Cliff	3	3	50
Sagebrush	6	12	33
Rock Slide	2	5	28
Forest	3	10	23
Alpine vegetation	1	6	14
Average index of restriction—33.			

Likewise, the relative degree of restriction of the belt faunae may be expressed and illustrated in the same way:

Vegetation belt	Restricted species (<i>R</i>)	Wide ranging species (<i>R'</i>)	Index of restriction $\left(\frac{R}{R + R'}\right)$
Sagebrush	13	19	40
Alpine	1	9	10
Spruce-fir	1	22	4
Pine	1	27	3
Average index of restriction—14.			

If the Spruce-Fir and Pine Belts are considered together as the Coniferous Forest, the situation is but slightly altered, for 5 species are restricted to the forest and 23 are wide-ranging, yielding an index of restriction of 17. This increases the average to but 22. If, however, the total faunae of the three upper belts are considered as belonging to the Mountain Slope Zone and compared with the fauna of the Sagebrush Belt or Plains Zone, a faunal zonation is revealed as follows:

Zone	Restricted species (<i>R</i>)	Wide ranging species (<i>R'</i>)	Index of restriction $\left(\frac{R}{R + R'}\right)$
Plains	13	21	38
Mountain Slope	10	21	32
Average index of restriction—35.			

The average indices of relative restriction for the communities and zonal faunae are about two and one-half times as great as that for the belt faunae. Hence, comparing the relative degrees of restriction of the three groupings, it is evident that the communities and the zonal faunae show more evidence of mammal restriction in this region than the belt faunae. The fact that a zonal fauna includes a number of communities which in themselves are relatively restricted in composition, points to the conclusion that the community in this case is the most applicable grouping in classifying the mammal distributions.

Similar tests as these may very well be applied in the field in order to determine graphically the relative values of different groupings or schemes of classifying distributions, each of which is based upon some conspicuous factor in the environment.

Nichols (1930), in reviewing the present day tendencies of European plant ecologists, notes that the Swiss-French school advocates a test which they apply to the plant community and which they designate by the term

"Exclusiveness." By this is meant the degree in which a species is restricted to one particular community to the exclusion of others. This is somewhat comparable to the degree of restriction described in this paper, although it does not necessarily involve an index. The Swedish school, however, does not consider the test of "Exclusiveness" of any ecological significance.

Allen (1878) in a like manner compared the numbers of indigenous genera and families with the number of cosmopolitan ones in classifying zoogeographical realms, regions and provinces.

The purpose of the index of restriction as described is to compare the different schemes or groupings of classification of mammal distribution. Each scheme should be based upon some outstanding factor in the environment such as topography, temperature, humidity or vegetation in order that the applicability or significance of these factors may be determined. Hence, much depends upon the sane judgment of the individual in picking out the conspicuous factors in the environment upon which to base his schemes. The greater the number of schemes used, the less chance there is of missing an important factor in that region. For instance, if the distributions of the mammals of a region should be classified according to ten different schemes based upon ten different factors in the environment and three of these should be found to have equally high average indices of restriction, then it would be legitimate to conclude that of all the factors considered, these three were relatively the most significant in determining the distributions in that region. There seems no reason why this index of restriction may not be applied to any group of animals, the distributions of which can be classified according to different schemes based upon different predominating factors in the environment.

DIFFERENT CLASSIFICATIONS OF THE VEGETATION BELTS

Although the vegetation belts do not show any great degree of mammal restriction in the Uinta Region they are very conspicuous. Table II compares the classification of the vegetation belts adopted by the writer for the northern slope of the Uinta Mountains with similar classifications for the states of Utah and Nevada (Tidestrom, Shantz, and Sampson in Tidestrom, 1925; Cottam, 1929; and Nord, 1929). No two authors agree exactly. Tidestrom, Shantz, and Sampson all deal with Utah and Nevada and yet disagree in minor respects. Cottam deals with Utah only and agrees in different details with these three authors. Nord, in conjunction with the United States Forest Service, has compiled a classification based more particularly, I judge, upon the southern slope of the Uinta Mountains. He distinguishes two separate pine belts where I have but one and gives the juniper-pinyon belt equal ranking with the other belts. In general these classifications are comparable and where they are not, the name of the belt so indicates. Such a system is flex-

ible and extremely useful in comparing regions and showing the altitudinal zonation of plants.

CONSIDERATION OF CERTAIN CONCEPTS

THE MAMMAL COMMUNITY AND HABITAT

In this study the term association has been avoided as much as possible owing to the fact that it has recently come to have almost as many meanings as the number of persons using it (Clements, 1916; Gleason, 1926; Nichols, 1929). The more noncommittal terms, habitat and community, are used in its place. Even these terms have come to connote different meanings to different people. It will be necessary, therefore, to state the sense in which these terms are used here. The term habitat is used as meaning a definite type of area characterized by easily recognizable and relatively constant features. For instance, the rock slides constitute one habitat, or, as some may prefer to call it, a habitat-type, in counter-distinction to what is sometimes called a unit habitat. The communities which inhabit these habitat-types are likewise type communities inasmuch as certain characteristic forms are always found in these habitats although other forms may be added to or subtracted from the habitats as they are repeated or duplicated. The community-type is, therefore, relatively constant in regard to its habitat-type. It will be understood, then, that as the terms are used here, the mammal communities and habitats are referred to in the sense of type communities and type habitats.

As the habitat is repeated in different vegetation belts and so at different altitudes, the community which it shelters may become modified and so differ in composition—additional species may occur or some may drop out. Often a mixed habitat results in an intermediate region. For instance, where the trapping station was maintained on Sheep Creek (Fig. II), the altitude and surrounding vegetation indicated the Sagebrush Belt. However, constituents of both sagebrush and upper belt fauna and flora (see p. 56) were found there. The community, then, is modifiable but must have some degree of habitat restriction to be retained as such in the present classification.

COMPARISON WITH THE PLANT ASSOCIATION

Inasmuch as the community is considered here as occupying a definite habitat which becomes a workable unit in classifying distributions, it may be compared with the recently much disputed concept of the plant association. Gleason's (1926, p. 23) idea is that of a concrete association which is brought about as "the resultant of two factors, the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment." Hence, it is not analogous to an organism nor can it be considered a unit of vegetation. Clement's viewpoint (1916, pp. 124-129) involves the inevitable attain-

ment of a climax—the result of progressive successions—which is comparable to an organism in that it is subjected to the same developmental laws. His term association is restricted to the climax communities which make up the formation. Nichols (1929, p. 637) takes the very sane viewpoint of regarding the plant association as “a piece of vegetation which exhibits essential uniformity in floristic composition and ecological structure.” It may be regarded in either an abstract or concrete sense but it is primarily a definite “fundamental unit of ecological plant sociology.” He compares it with the species concept which varies notoriously in the opinions of different systematists. However, as he pertinently remarks (p. 631) “is absence of general agreement . . . any more reason for discarding our concept of the species as a floristic unit?” The mammal community, as it is used and defined here as a distributional unit, agrees closely with Nichols’ view of the association. However, in regard to the causes which bring it about, Gleason’s idea of the plant association depending upon the coincidence of immigration and the environment for its existence resembles, in my opinion, my idea in regard to the factors responsible for the composition of the mammal community. The mammal community at any one time is the result of a complex of interacting factors which are constantly producing changes and of which one or several may be more in evidence at that time.

ZONAL INFLUENCE

Altitudinal zonation of the vegetation is conspicuous on the mountain slopes of the western United States. This is particularly true of the northern slope of the Uinta Mountains. The broad vegetation belts are prominent regardless of the fact that they interdigitate and overlap (Fig. II). There are also two broad topographic zones in this region, the Plains Zone and the Mountain Slope Zone, as well as various types of habitats. It has been shown (p. 62) that the zones and habitat-types have a greater degree of mammal restriction in this region than do the vegetation belts. It was also shown that the habitat-type is the logical grouping in classifying the mammal distributions in this region. This view may be substantiated by considering the repetition of the habitats in the different belts and zones. Where the habitat of a mammal community recurs in a different vegetation belt, characteristic members of the community also recur. Thus, a type of habitat is established. For instance, the Rock Slide Habitat-type appears in the Pine, Spruce-Fir and Alpine belts. The pika, marmot and two species of chipmunks are found in this habitat-type regardless of the belt. This illustrates the predominating influence of the habitat-type over the vegetation belt. It is only when the habitat is restricted to a definite belt that the community is also restricted, *i.e.* the Rock Cliff Habitat and Community; the Alpine Vegetation Habitat and Community. Likewise, the habitat-type is transcendent in influence over the topographic zone. The Stream-side Habitat-type occurs in both the Plains

and Mountain Slope Zones. Such characteristic members of this habitat-type as the beaver, muskrat, mink, meadow mouse and shrew also recur. The Sagebrush Habitat-type appears in both zones. The deer mouse, badger and jack rabbit are similarly associated with it regardless of zone.

Field naturalists who use the life-zone system of classifying animals and plants usually find that the plants fit into this classification fairly well, chiefly on account of the fact that the life zones are based in part upon the plant indicators. However, they experience far more difficulty in forcing the mammals and other vertebrates into such a scheme. Many authors, although describing animal distribution as based primarily upon life zones, have used habitats or associations for a more adequate determination of the vertebrate distributions.

Grinnell and Storer (1924, p. 9) state, "Frankly we found difficulty in assigning some parts of the Mono portion of the Yosemite section to one life zone rather than to another." Again (p. 11), "the limitation of species on the life-zone concept is not the only sort of segregation which occurs . . . often a far more conspicuous manner of delimitation is manifest, the delimitation which takes place on the basis of 'associations.' . . . Not rarely, associational restriction seems to be transcendent over zonal restriction."

Taylor (1922, p. 216) says, "A combination of the life zone, mapped on broad lines with temperature as the basic factor, and the habitat with its association, determined chiefly on water relations, should afford a more adequate picture of the distribution of plant and animal life on Mount Rainier than would either alone."

Cary (1911 and 1917), in applying life zones to the fauna and flora of Colorado and Wyoming, does not list any convincing number of animals, of mammals at least, which could be used in determining the upper life zones. All of the life zones recognized by him show a high degree of overlapping, especially in respect to the mammal fauna. Howell's life-zone classification of Alabama (1921) has been criticized by Dice (1923) as another illustration of forcing nature into pigeon-holes. The indefiniteness of life zones is often the rule rather than the exception in the field. Dice (1916), Grinnell and Storer (1924), Grinnell (1914), Taylor (1922), Allee (1926), and others have all encountered it.

In the Uinta region, Merriam's life zones cannot be applied, for temperature data are lacking or incomplete and the plants which are supposed to characterize the different life zones are not always in their proper places. Cottam (1930), speaking of the flora of the Uinta Mountains, says, "Some of the best examples of zone jumbling to be found in Utah are furnished by this region, . . ." Even granting that in regard to the plant life alone, the vegetation belts as described here may be considered as approximating life zones, certain difficulties are confronted. For instance, Cary (1917) includes lodgepole pine in the Canadian zone whereas in the Uinta region this pine and

the yellow pine present a distinctly mixed forest. Hence, the pine belt could be called "transition" because of the yellow pine or "canadian" because of the lodgepole pine. In regard to the mammal distribution of this region, life zones cannot be applied, for, it has been shown that the mammals here are restricted in their distributions primarily by their habitat relationships and without regard to plant zonation.

SUMMARY

1. Field data concerning the ecological distribution of the mammals on the north slope of the Uinta Mountains were secured and classified according to three schemes, namely, topographic zones, vegetation belts, and habitat-types.

2. A test for the relative values of these three schemes involving an index of restriction and consisting of the ratio of restricted to ranging forms, is described and applied to the data secured in this region.

3. By means of this test, it is found that the mammal habitat-types and the community-types indicate the greatest degree of restriction and so form the most logical grouping for classifying the mammal distributions.

4. The mammal community and habitat is used by the writer in the sense of a type community and habitat and as such may be considered comparable to the plant association as determined by Nichols (1929, 1930).

5. The life-zone system of classifying distributions is found to be inapplicable to the mammals, at least in the Uinta region.

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TABLE I. *Climatological Data for Manila, Utah.*

7 YEARS	Temperature °F.											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean.....	17.7	23.2	31.8	39.9	47.5	57.9	65.4	63.2	54.4	50.0	32.0	18.2
Mean maximum.....	33.1	37.6	46.2	53.9	62.5	74.5	82.9	81.7	71.6	60.7	47.8	32.6
Mean minimum.....	2.3	8.7	17.3	25.8	32.5	42.0	47.9	14.8	37.1	29.2	16.2	3.8
9 YEARS												
Highest.....	62.0	59.0	68.0	77.0	86.0	95.0	89.0	95.0	88.0	82.0	73.0	64.0
Lowest.....	-32.0	-31.0	-14.0	-6.0	15.0	25.0	30.0	33.0	19.0	-3.0	-20.0	-28.0
	Precipitation, inches											
10 YEARS												
Mean.....	0.37	0.53	0.48	1.65	1.15	0.73	1.04	.065	1.10	1.46	0.50	0.43
Mean maximum.....	1.00	1.15	1.17	2.95	3.62	2.00	1.94	1.24	2.95	2.24	1.02	1.01
Mean minimum.....	T	T	0.11	0.39	0.28	0.15	0.55	0.13	0.14	0.22	0.03	0.05
8 YEARS												
Snowfall.....	5.00	7.20	4.30	8.10	1.80	0	0	0	0.40	1.90	4.00	7.40

(T means trace)

Frost Data.

8 YEARS

Average date of last killing frost in spring June 22
 Average date of first killing frost in autumn..... Sept. 8
 Average length of frostless season..... 78 days (127 days for Vernal)

10 YEARS

Longest frostless season..... 106 days
 Shortest frostless season..... 59 days

TABLE II. *Classifications of Vegetation Belts.*

Svihla	Nord	Cottam	Tidestrom	Shantz	Sampson
Alpine 11,700-11,900 meadow krumholz	Alpine	Alpine Grassland 10,000 and above	Alpine	Alpine Grassland	Arctic-alpine
		Spruce-fir 8,000-10,000	Subalpine		
Spruce-fir 10,500-11,700	Spruce-fir	Aspen	Spruce	Spruce-fir Forest	Spruce-fir
		Spruce-fir 7,000-8,500	Aspen		Aspen-fir
Pine 8,000-10,500	Aspen-lodge- pole pine	Western yellow 5,500-8,000 pine	Yellow pine	Western yellow pine	Yellow pine and oak brush
	Western yellow pine	Scrub oak 5,000-7,500			
(Cedar-pinyon minor belt 7,000-8,000)	Juniper- pinyon	Pygmy forest 4,000-7,000	Pinyon	Pinyon- juniper woodland	Pinyon- juniper
Sagebrush 5,800-9,000		Northern desert shrub 3,500-5,000	Sagebrush	Northern desert shrub	
		Salt desert shrub 1,800-3,500		Salt desert shrub	
		Southern desert shrub 1,800-3,500	Creosote bush	Southern desert shrub	

TABLE III. *Animals in Zones, +, restricted to habitat-type; —, specimens, signs or observations; (), reports or general knowledge.*

Topographic Zones Species in Plains Zone only	Vegetable Belts											
	Sagebrush			Pine				Spruce-fir			Alpine	
	Streamside	Rock Cliff	Sagebrush	Streamside	Sagebrush	Rock Slide	Forest	Streamside	Rock Slide	Forest	Alpine	Rock Slide
<i>Lutra c. canadensis</i>	(+)											
<i>Spilogale</i> sp.....	(+)											
<i>Mephitis hudsonica</i>	+											
<i>Citellus armatus</i>	+											
<i>Sylvilagus nuttalli grangeri</i>	+											
<i>Eutamias m. minimus</i>	+											
<i>Eutamias dorsalis utahensis</i>		+										
<i>Peromyscus crinitus auripectus</i>		+										
<i>Peromyscus boylei rowleyi</i>		+										
<i>Cynomys l. leucurus</i>			+									
<i>Perognathus parvus clarus</i>			+									
<i>Dipodomys</i> sp.....			+									
<i>Antilocapra a. americanus</i>			(+)									
Species common to Plains and Mt. Slope Zones												
<i>Thomomys pygmaeus</i>	+			+								
<i>Sorex palustris navigator</i>	+			+								
<i>Mustela vison energumenos</i>	+			+				+				
<i>Castor canadensis frondator</i>	+			+				+				
<i>Microtus n. nanus</i>	+											
<i>Microtus m. mordax</i>	+			+				(+)				
<i>Ondatra zibethica osoyoosensis</i>	+			+				+				
<i>Taxidea t. taxus</i>			+		+							
<i>Lepus t. townsendii</i>			+		(+)							
<i>Sciurus f. fremonti</i>												
<i>Erethizon e. epixanthum</i>							+			+		
<i>Callospermophilus l. lateralis</i>							+			+		
<i>Peromyscus maniculatus osgoodi</i>	—	—		—	—	—	—					
<i>Lynx uinta</i>	—	—		—	—	—	—					
<i>Canis l. lestes</i>	()		—	—	()		()	()		()		
<i>Eutamias minimus consobrinus</i>	—		—	—	—	—	—	—		—	—	
<i>Eutamias umbrinus</i>	—			—	—	—		()	()		—	—
<i>Odcoileus h. hemionus</i>	—		()	—	—	—		—	()		—	—
<i>Felis oregonensis hippolestes</i>	—		()	—	—	—	—	—	—	—	—	—
<i>Neotoma cinerea orolestes</i>			()	()	()		()	()	()	()		
(Bison b. bison) formerly ranging throughout this region.												
Species in Mt. Slope Zone only												
<i>Zapus p. princeps</i>				+								
<i>Marmota flaviventris nosophora</i>						+		(+)				+
<i>Ochotona princeps uinta</i>						+		+				+
<i>Glaucomys sabrinus bangsi</i>							+			+		
<i>Clethrionomys gapperi galei</i>								+				
<i>Thomomys</i> sp.....											+	
<i>Euarectos a. americanus</i>				—	—		()	()		()		
<i>Ursus horribilis</i>				()	()		()	()		()		
<i>Lepus b. bairdi</i>					—		—	()		—	—	
<i>Cervus c. canadensis</i>				()	—		—	()		—	—	



FIG. 1. Map of northeastern Utah and parts of Wyoming and Colorado showing location of Wasatch and Uinta Mountains (after Atwood, 1909).

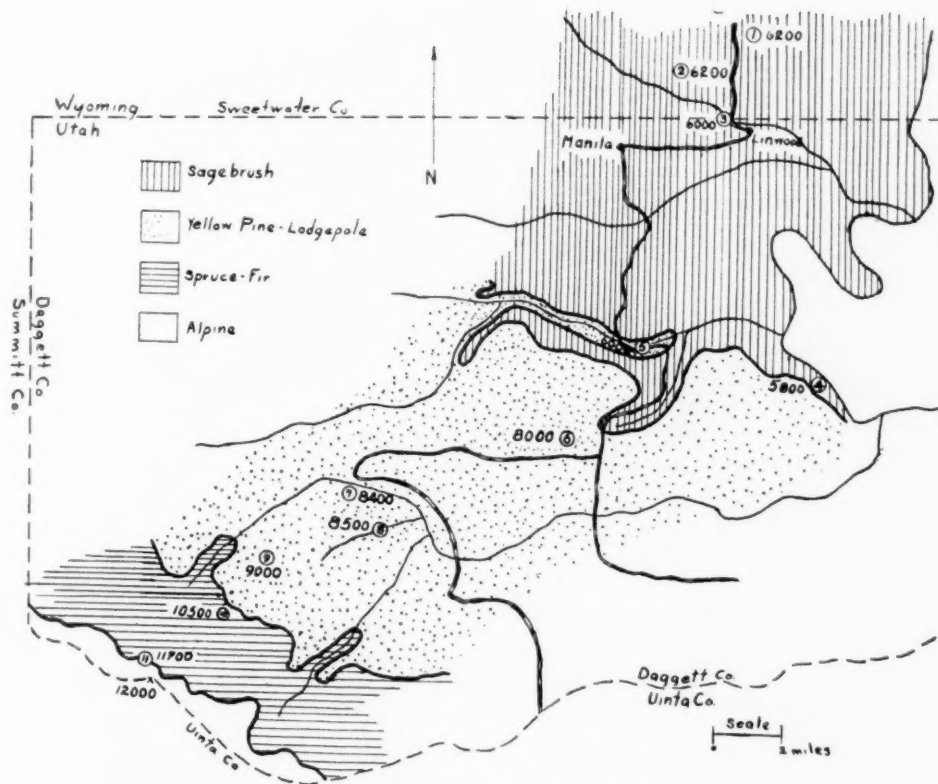


FIG. 2. Detail map of Daggett County, Utah and Sweetwater County, Wyoming, showing dominant vegetation belts, important creeks and rivers, and the following collecting stations with their respective altitudes: (1) Two miles north of Linwood, Utah; sagebrush plains. (2) One mile north of Linwood, Utah; rock cliff habitat and petroglyph rocks. (3) Henry's Fork; streamside habitat, sagebrush belt. (4) Hide Out; streamside habitat, sagebrush belt. (5) Sheep Creek; mixed habitat, sagebrush belt. (6) West of Summit Springs; mountain park, pine belt. (7, 8) Beaver Creek; mountain park, pine belt. (9) Granite Park; mountain park, pine belt, approximate upper limit of sagebrush and deer mouse. (10) Beaver Dams; streamside habitat, spruce-fir belt. (11) Timberline on the Nipple; alpine belt.

*TRANSECT of NORTH SLOPE of UINTA MTS.
Showing Dominant Vegetation Belts and
Topographic Zones*

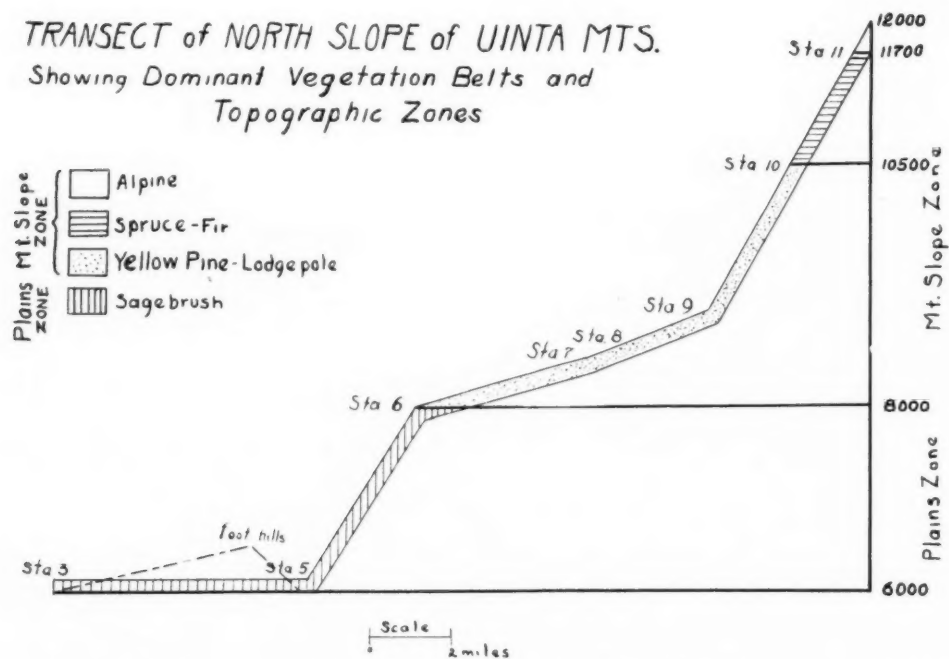


FIG. 3. Ideal transect of the north slope of the Uinta Mountains, Utah, showing profile of the mountain slope, vegetation belts, topographic zones, collecting stations and altitudes.



FIG. 4. Sagebrush Habitat of the Sagebrush Vegetation Belt, 2 miles north of Linwood, Utah, (6200 feet), Station 1 (Fig. 2). Typical habitat of such mammals as the prairie dog, pocket mouse, deer mouse, coyote, jack rabbit and, formerly, the antelope.



FIG. 5. Prairie dog in a prairie dog town on a flood plain of Green River, near the mouth of Henry's Fork.



FIG. 6. Collecting Station 5 (Fig. 2) on Sheep Creek, 6000 feet altitude, showing character of the canyon, a mixed habitat where upper belt flora and fauna mingle with lower belt forms. Cedars dot the canyon slopes.



FIG. 7. Talus slope of Rock Cliff Habitat on Sheep Creek canyon showing steepness of the slope. Cedars and sagebrush have become established here. This is the habitat of the golden-breasted canyon mouse.



FIG. 8. Upper Sheep Creek canyon showing Douglas firs which extend down into the Sagebrush Belt along such cool canyons.



FIG. 9. Sagebrush in a mountain park in the Pine Belt, 8500 feet altitude. Station 8 (Fig. 2), showing dense lodgepole-pine forest in the background and sagebrush in the foreground.



FIG. 10. Mountain park at Beaver Creek (8500 feet) looking towards the Nipple, which is the peak at the right; grassy flood plain subhabitat of the pocket gopher in the foreground, which is sharply marked off from the sagebrush. Lodgepole and yellow-pine forest in the background.



FIG. 11. Beaver house on Beaver Creek near Collecting Station 8 (Fig. 2). Muskrats had built a house on the right hand side of this.



FIG. 12. Elk Park in the Pine Belt at 8000 feet altitude, showing willow subhabitat of the jumping mouse.,



FIG. 13. Elk Park showing open growth of western yellow pine.



FIG. 14. Hoary marmot, *Marmota flaviventris nosophora*, in a rock slide of the Pine Belt.



FIG. 15. Creek at Beaver Dams, Station 10 (Fig. 2), at 10500 feet altitude in the Spruce-Fir forest. The Nipple is the peak in the distance.



FIG. 16. Timberline (11700 feet) on the Nipple, looking back on the Spruce-Fir forest.



FIG. 17. Pika or coney, *Ochotona princeps uinta*, on a rock slide above timberline on the Nipple.



THE ECOLOGY OF CERTAIN FISHES AND AMPHIB-
IANS WITH SPECIAL REFERENCE TO THEIR
HELMINTH AND LINGUATULID
PARASITES

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THE ECOLOGY OF CERTAIN FISHES AND AMPHIBIANS WITH SPECIAL REFERENCE TO THEIR HELMINTH AND LINGUATULID PARASITES

INTRODUCTION

The ecology of parasites, though it offers an attractive field for research, has been little promoted by science. "It is to be hoped that it will be increasingly cultivated by scientific men. It should yield rich harvests, not only to scientists and scholars, but also to those who are interested in commerce and the advancement of the human race" (Pearse 1926). In this paper the writer has attempted a study of certain animals with special reference to the ecology of their parasites.

Thanks are due to Professor A. S. Pearse under whose direction this study was made and whose assistance and helpful suggestions have made this work possible; to Professor H. J. Van Cleave who identified the acanthocephalans; to Professor H. W. Stunkard for helpful suggestions on the trematodes; to Professor D. W. Rumbold and Miss Sophie Dehler who assisted in collecting and examination of many of the hosts.

ECOLOGY OF PARASITES

Linton (1910) states that, "There does not appear to be evidence of any marked periodicity in the occurrence of helminth parasites of marine fishes, either adult in the alimentary canal or miniature encysted in the tissues of their hosts, beyond what may be expected where fishes are exposed to varying course of migration." Conditions of life in freshwater are usually more varied than in the ocean and, therefore, one would expect to find seasonal changes and greater variation in the infestation of freshwater hosts.

Van Cleave (1916) studied the seasonal variation in three species of acanthocephalans, *Neoechinorchynchis emydis* (Leidy), *N. gracelesentis* Van Cleave, and *N. longiostris* Van Cleave. The first species, a parasite of the turtle, showed no seasonal variation but the last two demonstrated definite seasonal cycles. *N. gracelesentis* enters the gizzard-shad in summer, reaches maturity by mid-winter, and disappears entirely during spring and fall. Van Cleave states that he believes the variations he described were due to seasonal changes in food habits of the host or to active migrations of the hosts from or to the sources of infection.

Cort (1922) found that a lowering of the temperature caused a decrease in the number of cercariae escaping from a snail and that some species of snails liberated more cercariae at night while others reached a maximum during the day. McCoy (1928) studied the infestation of *Planorbis trivolvis* with larval trematodes and found that the infestations varied widely but did not observe

clear cut seasonal fluctuations. McCormick (1923) made comparative studies of the parasites of certain freshwater snails in which the percentages of infestation varied from 14.5 to 0.0 per cent. Miller and Northup (1926) reported seasonal variation of larval trematodes in the marine mollusc, *Nassa obsoleta*.

Linton (1910) reported on the comparative parasitism of marine fishes at Woods Hole, Mass.; Beaufort, N. C.; Bermuda; and Tortugas Florida. Woods Hole has many fishes typical of the northern waters; Beaufort is characteristic of the warm temperate zone and includes some fishes which occur also at Woods Hole; Bermuda, in the open sea, has an equable climate and a large number of coral reef fishes were collected there; and the Dry Tortugas, situated near the Tropic of Cancer, is in the Gulf Stream and surrounded by coral reefs. Linton found differences in the parasites of these regions. He found a wide distribution of immature encysted stages of various species but a more restricted range for adults. Acanthocephalans were more frequent in colder waters and the same was true to a lesser degree of cestodes and nematodes. The trematodes appeared to increase in hosts living in the warmer waters.

Ward (1909) reported that *Rana pipiens* Schreber had its maximum number of intestinal helminth parasites during its hibernating period and that the number decreased during spring and summer. He concluded that parasites hibernated with the host. This view differs from that of Blanchard (1903), who studied hibernating marmots and found an absence of helminth parasites in the intestine. He suggested that this may be due to the reduction of the body temperature of the host. Hausman (1897) found that European perch had few trematodes in the spring. This he attributed to the fact that the fishes were eating little because of the extreme cold. Pearse (1924) reported that the American perch has a high infestation during the winter although it eats little if any food. Essex (1927) found the tapeworm *Corallobothrium* of catfish reached its maximum infestation during June and July.

Parasites may enter a host in many ways: (1) with the food, (2) by active migrations to and into the host, (3) by accidental contamination from bottom mud, vegetation, or other materials, and (4) by inoculation. Mrazek (1891) and Van Cleave (1920) found parasites encysted in amphipods. Pearse (1924) found that the fishes which feed largely on amphipods are highly infested with the parasites these crustaceans carry. Many parasites occur encysted in fishes and the fish-eating fishes are highly infested. For example, freshwater dogfish, wall-eyed pike, and gar feed largely on fish and carry large numbers of parasites (Pearse 1918).

There are many scattered papers in which incidental reference is made to the parasitism of various aquatic animals. Among these may be mentioned those by La Rue (1914), Marshall and Gilbert (1905), Ward (1910), and Pratt (1923).

Van Cleave (1919) reported that half the species of fishes from Douglas Lake, Michigan, were infested with acanthocephalans. Kelly (1899) concluded that the *Unionidae* exhibited unlike capacities for infestation due to such factors as age, size of host, size of stream, and density of population. Linton (1899) found that eels caught in the sea harbor a parasitic fauna characteristic of the sea and only a few freshwater species. Zschokke (1902) found that the lawyer, *Lota vulgaris* L., the only freshwater representative of a typically marine family of fishes, possessed very few parasites characteristic of freshwater fishes but harbored many parasites which occur rarely in freshwater animals. He also reported that salmon lost a large number of their parasites during their migrations up the Rhine and Ward (1909) also found the Alaskan salmon acquired a copepod, never found in salt water, during its migrations inland.

Essex and Hunter (1926) found that thirty-nine percent of the fishes studied from the upper Mississippi and Missouri basins showed infestation with parasites, and reported a lesser percentage of parasitism in river than in lakes; the former averaging 24 percent more than the latter. Pearse (1924) discussed the abundance of parasites in five Wisconsin lakes. He found that Lake Mendota, a stratified inland lake, contained fewest parasites and Lake Pepin, which is an expansion in the course of the Mississippi River, had the greatest number of parasites. The lake (Michigan) with the widest range of territory and the greatest variety of habitats had the highest average infestation per fish. Lake Pepin, with a sandy bottom, warm water, and lack of marked thermal stratification, had twenty-two percent more parasites than Lake Michigan with its soft mud bottom and cold waters.

When one attempts a study of the parasites found in a particular host or locality, it is apparent that many ecological factors should be considered. Many of the problems in parasitology will be better understood when the scientist considers the biotic factors which influence the kinds of parasites and the degrees of infestation.

LOCALITIES WHERE COLLECTIONS WERE MADE

North Carolina is naturally divided into three great physiographic sections: the Coastal Plain, the Piedmont Plateau, and the Appalachian Mountain Region. Durham, N. C. is situated in the Piedmont Region. The geological formations show upturned belts of slates, granites, and other rocks. The erosion of these rocks of varying hardness has led to the development of cascades, rapids, and swift flowing streams.

Collections made near Durham were from the Eno River and from an old settling pond near the river. Some of the collections were also made from a mill race below a dam in the same river. The Eno river has its source in Orange County west of Hillsboro, N. C., and with other tributaries forms the

Neuse River. The settling pond studied is about a quarter of a mile from the river, is being rapidly filled with sediment, and emergent plants are beginning to invade it at both ends. This pond is about forty years old and has a length of about one-half mile, a width of about one hundred and fifty feet, and a depth of about ten feet. It is surrounded by a wooded area of yellow pine, maple, and elm trees.

An artificial lake at Lakeview, N. C., from which collections were made, is about twenty years old. It was formed by the damming of a small branch of the Cape Fear River about fifteen miles from the source, which is about five miles north of Pinehurst, N. C. The lake is about 0.2 of a mile wide and about 0.5 of a mile long. The surrounding section is in the western end of the Coastal Plain among sand hills, which before being cleared for cultivation were well forested with pines and gums. The water flowing through this sandy area is quite clear and has a slight amber tint. The upper end of the lake still retains many of the trees and stumps left from the wooded area which was flooded over to form the lake. There are tupelo gum and cypress trees along this shore. The shore along the middle of the lake slopes gradually and the sandy bottom is here being covered by a layer of muck which in some places is about a foot thick. A luxuriant growth of *Myriophyllum* occurs in many parts of the lake and fishes usually were collected from such areas. Along the sandy shores of this lake grow pitcher plants, some cacti, black jack pine, and long leaf pine.

The artificial lake near Gibsonville, N. C. is about one hundred years old and was formed by the damming of a small stream which flows into a branch of the Cape Fear River. This lake is about a quarter of a mile long and varies in width from about one hundred and fifty to two hundred feet. The bottom is covered with muck which is over a foot deep. The forest surrounding the shores consists mainly of deciduous trees with a few scattered pines.

HOSTS AND PARASITES

Hosts

After some preliminary collecting certain fishes and amphibians were selected for study. These were species which were characteristic of the particular habitat and could be obtained in sufficient numbers to permit routine examinations. Examinations were made during 1927 and 1928. The months during which each host was examined are given in Tables I-XIII.

The hosts studied were: the blue-spotted sunfish, *Enneachanthus gloriosus* (Holbrook); the pumpkinseed, *Eupomotis gibbosus* (Linnaeus); the yellow bullhead, *Ameiurus natalis*; the warmouth bass, *Chaenobryttus gulosus* (Cuvier and Valenciennes); the cricket frog, *Acris gryllus* (Le Conte); and the newt, *Triturus viridescens* Rafinesque.

PARASITES

Trematodes

Ancyrocephalus sp.: gills of warmouth, pumpkinseed, a blue spotted sunfish.

Brachyocoelium trituri Holl: intestine of newt.

Paramphistomum stunkardi Holl: colon of warmouth and pumpkinseed.

Opithodiscus americanus Holl: colon of newt.

Phyllodistomum carolini Holl: urinary bladder of warmouth and yellow bullhead.

Phyllodistomum pearsei Holl: urinary bladder of blue spotted sunfish.

Plagiorchis ameiurensis McCoy: intestine of yellow bullhead.

Plagitura salamandra Holl: intestine of newt.

Diplostomum cysts: skin and fins of warmouth and pumpkinseed.

Strigeid cysts: liver, mesenteries, and uterus of warmouth, pumpkinseed, and blue-spotted sunfish.

Nematodes

Capillaria sp.: intestine of newt.

Cosmocerca dukae Holl: colon of newt.

Spinitectus carolinus Holl: intestine of warmouth and pumpkinseed.

Spiruroid worms: intestine of blue spotted sunfish.

Philometra cysts: mesenteries, walls of stomach and intestine of pumpkinseed, warmouth, blue-spotted sunfish, and newt.

Acanthocephalans

Acanthocephalus acutulus Van Cleave: intestine of newt.

Neoechinorchynchus cylindratus (Van Cleave): liver and mesenteries of blue-spotted sunfish.

Cestodes

Corallobothrium giganteum Essex: intestine of yellow bullhead.

Protocephalus cysts: mesenteries of blue-spotted sunfish.

Linguatulid

Bdulus ichthyus Holl: swim-bladder, liver, and mesenteries of yellow bullhead.

SEASONAL VARIATION IN THE NUMBER OF PARASITES
TRITURUS VIRIDESCENS

At Durham, N. C. this salamander was found to contain the following parasites: *Acanthocephalus acutulus*, *Capillaria* sp., *Cosmocerca dukae*, *Opithodiscus americanus*, *Plagitura salamandra*, and *Philometra* cysts. The seasonal variations in the occurrence of these parasites are shown in Tables

I and II and in Figs. 1 and 2. The newt has a high percentage of its individuals infested and the percentage never fell below fifty per cent. A broken line is used on the graphs between April and June since during May only two individuals were collected. No salamanders could be found during August. The writer has found that during certain months it is difficult to collect the aquatic stage of the newt and this may be due to the fact that part of the life cycle is spent in the water and part on land.

The average number of hosts infested was lowest during the summer months. There was a slight decrease in the winter but not to as low a level as the average for the summer. *Acanthocephalus acutulus* did not appear until September and the percentage of hosts infested was high during the winter. The average infestation per host reached its maximum during October and decreased during winter and spring. The percentage infested with *Capillaria* sp. was variable, being highest in September and November. The average infestation with this parasite varied and there is no apparent seasonal periodicity. *Cosmocerca dukae* was abundant during the fall and decreased through the winter months. The average infestation when plotted forms an interesting curve which rises from June until October and falls during the winter and spring. *Opithodiscus americanus* showed no particular seasonal periodicity. *Plagitura salamandra* has a low percentage and low average infestation during the summer.

Acanthocephalans have only once been reported from North American amphibians, although they occur frequently in Europe. Van Cleave (1915) reported seven worms from *Triturus viridescens* collected near Baltimore, Md. in 1893. He also discussed examinations made by investigators of recognized ability on over three-hundred amphibians from nine middle western states without finding acanthocephalans. The writer has examined salamanders from Indiana and New York with the same results. It is probable from these facts that acanthocephalans are either rare as parasites of amphibians, or have a limited seasonal cycle and only appear in hosts collected at the proper season. Acanthocephalans were not found in newts collected at Lakeview or in other species of salamanders collected at Durham.

The study of seasonal variation of parasites of *Triturus viridescens* is made difficult by the habits of this salamander. The degree of parasitism differs in those living on land from those in the water. In compiling the data in Tables I and II only salamanders with aquatic characteristics were used. The parasites of the different stages in the life cycle will be discussed later.

ACRIS GRYLLUS

Cricket frogs were studied from March 1927 to April 1928. During the months of December, January, and February none were secured. This frog was found to contain nematodes in the lungs and intestine and tapeworms in the intestine. The species of these parasites have not been identified.

The seasonal periodicity in this frog is shown in Table III and in Fig. 3. The parasites decreased in number from March to July and were absent from August to November. The frogs were again infested when collections were made in March, 1928 and increased in April. In the table the average sizes of the frogs examined during each month are given, because during the summer and autumn the individuals were smaller. Those less than 15 mm. in body length were without parasites. The small frogs were collected during the season when parasites were absent from even the large individuals. This species of frog showed a decided seasonal variation. Apparently it became infested during the season when it entered the water for breeding and lost its parasites during the summer and winter. The nematodes increased during the breeding season and decreased when it was over. The tapeworms were present in April and May, 1927 and absent until April, 1928.

CHAENOBRYTTUS GULOSUS

Warmouth bass were collected from the settling pond near Durham, N. C. This fish was infested by *Ancyrocephalus* sp.; *Paramphistomum stunkardi*, *Spinitectus carolinus*, Philometra cysts, and strigeid cysts. Tables IV and V show respectively the percentage of fishes infested and the average number of parasites per fish. The seasonal fluctuations of the parasites are shown in Figs. 4 and 5. In the warmouth bass a large number of the individuals were parasitised; the lowest was 50 per cent in May, 1927. The average infestation showed a gradual increase from April to August, when the maximum was reached, and dropped off again in October to remain low through the winter and spring.

Ancyrocephalus sp. appeared on the gills during March and April, 1928. *Paramphistomum stunkardi* had no apparent seasonal fluctuation in the percentage of hosts infested, although the average number per host was high during the autumn and again during spring. The average number of Philometra cysts reached its maximum during November; the highest percentage of infestation appeared during fall and winter; the parasite was absent during the summer. The percentage of hosts infested with *Spinitectus carolinus* was variable but the average infestation per host showed a decided increase during the summer. The percentage of hosts infested with strigeid cysts was highest in winter, there being a gradual increase to that maximum during the autumn. The highest average infestation occurred during the summer.

EUPOMOTIS GIBBOSUS

The pumpkinseeds collected from the settling pond near Durham were found to contain the following parasites: *Ancyrocephalus* sp., Philometra cysts, unidentified nematode cysts, and Diplostomum cysts. Figs. 6 and 7 and Tables VI and VII show the monthly occurrence of these parasites.

This fish was 100 per cent infested because of the presence of strigeid cysts in all specimens examined. The average infestation was variable and no periodicity was found. *Ancyrocephalus* appeared in March and April, 1928 as it did in the case of the warmouth bass. *Paramphistomum stunkardi* had its highest percentage of infestation during the autumn and the average per host reached its maximum during October. *Spinitectus carolinus* showed its highest percentage infestation during the winter and highest average per host during the spring. Unidentified nematode cysts which contained many larval worms were found in the intestine and mesenteries during the months of December, January, and February and were at their maximum during January. Diplostomum cysts were found in the skin and, from the data presented, apparently entered the fish in spring and left soon after.

ENNEACHANTHUS GLORIOSUS

The blue-spotted sunfishes were collected from the artificial lake at Lakeview, N. C. They were found to be infested with the following parasites: *Neoechinorhynchus cylindratus*, *Ancyrocephalus* sp., *Philometra* cysts, *Phyllodistomum pearsei*, spiruroid worms, protocephalan cysts, and an unidentified larval nematode. The data for this species are on Tables VIII and IX and the periodic occurrence is shown in Figures 8 and 9.

This sunfish showed its lowest infestation during the summer. The acanthocephalan, *Neoechinorhynchus cylindratus*, was first observed in December and was present during the remainder of time the observations were made. In April of the second year the average per host had dropped to four-tenths. *Ancyrocephalus* sp., was found on one fish in April, 1927. This trematode was not found again until March, 1928 and was absent the following month. The percentage of hosts infested with *Philometra* cysts was lowest during the spring, increasing during the summer and highest in winter. The average infestation per host reached its maximum in October. Protocephalid cysts appeared in September and were present throughout the winter; the percentage of infestation and average per host decreased between March and April. The spiruroid found in the intestine appeared to have two periodic cycles a year with the highest percentage and average infestation in spring and fall. The larval nematodes were absent during the summer months. Because of the large number of these worms and their small size only an estimate could be made of their number. They showed a gradual increase during the fall, a maximum in December, and a decrease in spring.

AMEIURUS NATALIS

The yellow bullheads used for observations given in this section were collected from the Eno River and the settling basin near it. They were hard to secure and none were obtainable from December, 1927 to April, 1928. This

fish was found to contain: *Philometra* cysts, *Phyllodistomum carolini*, *Plagiorchis ameiurensis*, and a corallobrothrid. The parasitism and monthly variation is given in Tables X and XI and in Fig. 10.

Large yellow bullheads were collected from the lake near Gibsonville, N. C., during November and December 1927 and again during March. These fishes contained a lingulatulid, and two trematodes, *Plagiorchis ameiurensis* and *Phyllodistomum carolini*. The phyllodistomes was absent in the fall but appeared again in the following spring. *Plagiorchis ameiurensis* was present in large numbers during the spring.

The percentage of hosts infested and the average number of parasites per host are both given, although the writer believes that the latter is a better criterion for the study of seasonal periodicity.

VARIATIONS OF PARASITES IN DIFFERENT HABITATS

FISHES

The variations in the parasites of the same species of fishes (sunfishes and bullheads) in three different habitats, the settling pond, Eno River, and the lake at Lakeview are shown in Table XII. The two lakes show a higher percentage of fish infested than does the river, although the river has a higher average per host than Lakeview. The higher infestations in the lakes may be due to the greater variety of habitats, greater environmental stability, and the presence of more animal associations.

Among the three artificial lakes studied that at Gibsonville is the oldest (100 years) and shows the highest parasitic infestation; the settling pond at Durham is next in age (40 years) and also in infestation; the lake at Lakeview is youngest in age and has a low degree of infestation. The smaller number of parasites in the last lake may be due to the presence of considerable areas of sandy bottom as well as the youth of the lake.

TRITURUS VIRIDESCENS

During October and November, 1927 salamanders with the aquatic characteristics and some which were transitional between aquatic and terrestrial stages were found. The average number of parasites per host in these two stages were compared with terrestrial individuals collected from under logs at the same time of the year. The data from these observations are summarized in Table XII. The infestation was low in the terrestrial eft; the transitional stage showed a slight increase; and the aquatic newts had many parasites. *Cosmocerca dukae*, *Opithodiscus americanus*, and *Acanthocephalus acutulus* are only found in the aquatic stage and apparently enter after the host returns to the water. *Plagitura salamandra* is present in all stages, although there is a marked structural difference in the appearance of this fluke in the eft and newt stages (Holl, 1928).

Triturus viridescens showed different trematode faunas at Durham and Lakeview although these two localities are only seventy miles apart. At Lakeview, which is in the Cape Fear drainage, *Gorgoderima intermedia* and *Brachycoelium trituri* are found, but at Durham, in the Neuse River drainage, the trematode parasites of the newt are *Plagitura salamandra* and *Opithodiscus americanus*. In both localities *Philometra* cysts, *Capillaria* sp. and *Cosmocerca dukae* occurred as nematode parasites in the newt. From the observation made in these two localities it appears that the trematodes have a limited area of distribution, or that there is an absence of the secondary hosts needed by the trematodes. Careful search failed to reveal any snails in the lake at Lakeview.

HOST SPECIFICITY

During the examination of pumpkinseeds and warmouth bass, collected in the settling pond at Durham, it was noticed that these two species of the family Centrarchidae contained the same parasites, but the pumpkinseed was more highly infested. The only parasites not occurring in both these species were Diplostomum cysts, which were found only on the pumpkinseed. Table XII shows the comparative infestation of the two species of fishes.

Ancyrocephalus sp. was an exception being more frequent in the warmouth bass. During the season of infestation 90 per cent of the warmouth bass were infested; compared to 35 per cent of the pumpkinseeds. During the months of March and April the average number of *Ancyrocephalus* per host was 9.6 for the warmouth bass and 0.9 for the pumpkinseed.

DISCUSSION

An ecological study of the parasites of two species of amphibians and four species of fishes has been described in this paper. The observations are based on the examination of 198 salamanders, 123 cricket frogs, and 388 fishes.

The newt, *Triturus viridescens*, has been shown to have its maximum infestation with parasites during the winter months. This agrees with the result of Ward (1910), who found similar conditions in the frog, *Rana pipens*. The seasonal occurrence of six species of parasites was studied in the newt and variations in seasonal periodicity were observed in three species.

At the beginning of its breeding season the cricket frog showed a very low infestation, which steadily increased during the breeding season. Following the breeding season there was decrease until autumn, when the frogs collected were entirely free of helminth parasites. The cricket frog apparently spends most of its time during the spring in the water and the writer's observations indicate that it becomes infested during the breeding period. The frogs collected during the late summer and autumn were smaller than in the spring, and it is possible that young frogs remain free from helminth parasites

until they enter the water to breed. However, the writer does not think this likely. He has frequently observed adult helminth parasites in the tadpoles of *Rana clamatans* Latreille.

The fishes showed a high infestation and the sunfishes studied showed a marked variation in the times of maximum average infestations. The warm-mouth bass had its maximum average per host during the summer months; the pumpkinseed was variable, there being no season showing a maximum infestation; and the blue-spotted sunfish had its maximum infestation during the winter months. Hausmann (1897) found few intestinal parasites in the European perch during the winter and concluded that this fish had fewer parasites during the winter because it ate less food at that season, but Pearse (1924) found that the American perch, which also ate little during the winter, was highly infested. The three centrarchids examined by the writer all ate less during the winter and the infestations showed specific variations. From these observations it appears that factors other than food enter into the periodicity of parasites. Several species of parasites showed seasonal fluctuations and in the pumpkinseed, in which no striking seasonal variation in the total average per host was observed, certain species of parasites nevertheless had periods of maximum infestation. *Ancyrocephalus* sp. appeared only in the spring, and certain nematode cysts were present only during the colder months. The bullheads showed an increase in average infestation during the fall and apparently reached the maximum during the winter. It is probable that some of the parasites which occur in fishes only in winter spend the remainder of their life cycles in hosts that may winter over as eggs, and the parasite occurs in fishes because it is forced to find a new host during the colder months.

The fishes collected in the Settling Pond and at Gibsonville were more highly infested than those from the Eno River. The lake at Lakeview had a lower infestation than the river but the lake is young having only recently overflowed its sandy shores. Essex and Hunter (1926) found lake fishes more highly parasitised than river fishes in their study of the Mississippi drainage system. Pearse (1920) found the same to be true in the case of fishes collected from the lakes and rivers of Venezuela.

The three artificial lakes studied were of different ages; Lakeview, twenty years; Settling pond, forty years; and Gibsonville, one hundred years. A correlated difference in the total infestation by helminth parasites was found. The number of parasites in the vertebrate population increased with the age of the lake. Pearse (1924) in his study of the parasites in five Wisconsin lakes found that the lakes with the widest variety of habitats had the highest infestation per fish. As lakes grow older they change their characteristics and many new types of habitats are formed. With the increase in variety of habitats new animal associations are formed and with these there is an in-

crease in parasites. The lakes arranged in the order of their average infestation per host are Lakeview (6.5), Settling Pond (12.8) and Gibsonville (35.8). A relationship is shown between the age of the lake and the parasites found in its fishes.

Many parasites require two hosts and will not appear until both hosts are present. At Lakeview a low infestation of trematodes was found and during the collecting no snails were discovered, although careful search was made. It is to be expected that as a lake grows older and more types of habitats are formed snails will become more numerous and the trematode infestation in the aquatic vertebrates will increase.

The fishes studied showed a considerable degree of host specificity. The pumpkinseeds and warmouth bass were collected from the same habitats and the pumpkinseed regularly showed a higher infestation. *Ancyrocephalus* showed a marked specificity for the warmouth while *Diplostomum* cysts were found only in the pumpkinseed. It is apparent that the pumpkinseed is the more usual host for most of the parasites which occur in the two species. Perhaps some of the differences in the parasitisms are due to different habits or habitats but in the present instance the pumpkinseed and warmouth were often collected in the same net and were found to feed upon the same foods. The difference in infestations may be limited, at least in part, by the presence of certain chemical substances in one species and the absence of these substances in the other.

Certain parasites are apparently limited to a particular drainage system. *Phyllodistomum superbum* Stafford is common in the urinary bladder of perch from the St. Lawrence drainage system, but Pearse (1924) examined several thousand perch from the Mississippi drainage and did not find it. He also records *P. fausti* Pearse from the Mississippi basin. A third species *P. staffordi* Pearse is known to occur in both the Mississippi and St. Lawrence systems. *Catoptroides lacustri* Lowen has been reported from the Mississippi system. *Phyllodistomum pearsei* and *P. carolini* are reported as occurring in the Atlantic drainage of North Carolina, *P. staffordi*, *P. carolini*, and *C. locustri* all occur in catfishes while *P. pearsei* and *P. fausti* are found in fishes of the Order Acanthopteri. As more data are collected it may be possible to work out a more detailed distribution of the genus *Phyllodistomum* in North America.

The nematode genus *Cosmocerca* contains three European species which are parasites in amphibians. *C. dukae* is the first and only species of this genus reported from the amphibians of North America. *Opithodiscus* has been reported as a European genus but during this study a new species *O. americanus* was found in the American newt.

Amphistome trematodes of the genus *Paramphistomum* have been reported from homoiothermic but not from poikilothermic vertebrates. During

this study *Paramphistomum stunkardi* was found in fishes. Daday (1907) reported amphistomes from South American fresh water fishes but none were in the genus *Paramphistomum*.

Linguatulids are representatives of a degenerate group of arachnids and have been reported from North American reptiles, birds and mammals, Dr. H. W. Stunkard has informed the writer that he has found linguatulids in the lungs of turtles. Two species of fishes collected at Gibsonville were found to be infested with this linguatulid.

There are many ecological factors which may enter into the study of parasitology and at present only the surface of this rich field of study has been scratched. In the future deeper delving will doubtless turn up an increasing number of facts which will have economic and scientific value.

SUMMARY

1. *Triturus viridescens* apparently has its minimum infestation during the summer because certain parasites show seasonal periodicity and are few or absent then.
2. Cricket frogs apparently become infested during the breeding season and have no helminth parasites during the remainder of the year.
3. The total infestation of centrarchids varies with the species of fishes studied. Certain parasites of centrarchids showed periodicity.
4. All parasites found in bullheads increased during the fall.
5. As artificial lakes grow older the average number of parasites in their vertebrate populations increase. This is in part, at least, probably due to the absence or presence of secondary hosts.
6. *Triturus viridescens* during its terrestrial stage has fewer parasites than when it lives in an aquatic habitat.
7. Newts from two different river drainage systems showed different trematode faunas but the nematodes were similar.
8. Pumpkinseeds have more parasites per individual than the warmouth bass collected from the same habitat.
9. An amphistome and linguatulid are reported from fishes of North America for the first time. Species of the genera *Cosmocerca* and *Opithodiscus* are reported as occurring in North America.

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TABLE I. *Triturus viridescens*: Percentage of Hosts Infested.

	Apr.	May	June	July	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Number of hosts examined.....	14	2	5	10	5	14	18	15	10	10	10	10
<i>Acanthocephalus acutulus</i>	57	50	100	90	100	93	89	93	90	100	100	90
<i>Capillaria</i> sp.....	0	0	0	10	60	64	55	13	40	50	30	30
<i>Cosmocerca dukae</i>	7	0	0	20	40	29	36	20	10	0	10	0
<i>Opithodiscus americanus</i>	29	50	60	30	40	43	45	13	20	60	50	20
<i>Philometra</i> cysts.....	0	0	40	10	40	64	11	13	20	30	60	30
<i>Plagitura salamandra</i>	50	0	40	20	60	64	72	87	60	60	70	80

TABLE II. *Triturus viridescens*: Average Number of Parasites per Host.

	Apr.	May	June	July	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Number of hosts examined.....	14	2	5	10	5	14	18	15	10	10	10	10
<i>Acanthocephalus acutulus</i>	0	0	0	0	1.2	3.2	.7	.3	1.2	.4	.2	.5
<i>Capillaria</i> sp.....	0	0	0	1.4	4	2.6	3.4	.9	2.1	3.1	.5	1.2
<i>Cosmocerca dukae</i>2	0	0	.3	.4	.6	.4	.3	.1	0	.1	0
<i>Opithodiscus americanus</i>	1.4	.5	3.6	.7	.4	1.8	2.6	2.7	1.1	4.6	2.7	1
<i>Philometra</i> cysts.....	0	0	1	.7	.6	2.1	1.4	1.1	.9	4.1	3.3	1.4
<i>Plagitura salamandra</i>	2.5	0	.6	1.4	2	2.3	3.8	5.1	1.8	3.4	4.5	1.8
Total average per host.....	4	.5	5.2	4	8.6	12.8	10.7	7.8	7.2	15.6	11.3	7.1

TABLE III. *Acris gryllus*: Percentage and Average Infestation.

	Number examined	Average size	Percentage infested	Average per host	Average Nematodes	Average Cestodes
March.....	6	33mm.	67	2.8	.5	2.3
April.....	11	30	55	1.8	1.5	.4
May.....	26	21	34	2	1.2	0
June.....	9	21	33	1	.3	0
July.....	10	18	10	.1	.1	0
August.....	10	15	0	0	0	0
September.....	14	16	0	0	0	0
October.....	10	16	0	0	0	0
November.....	11	18	0	0	0	0
March.....	5	16	20	.1	.1	0
April.....	10	19	70	4	2	2

TABLE IV. *Chaenobryttus gulosus*: Percentage of Hosts Infested.

	Apr.	May	July	Aug.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Number of hosts examined.....	7	4	6	6	12	10	10	10	10	10	5
Percentage of hosts infested.....	71	50	100	100	92	100	100	100	80	90	80
<i>Ancyrocephalus</i> sp.....	0	0	0	0	0	0	0	0	0	80	100
<i>Paramphistomum stunkardi</i>	0	40	0	33	8	20	40	0	20	10	20
<i>Philometra</i> cysts.....	0	0	0	0	50	70	60	30	20	40	40
<i>Spinitectus carolini</i>	57	20	20	67	25	40	50	60	30	50	60
Strigeid cysts.....	57	50	80	67	83	90	100	90	70	90	80

TABLE V. *Chaenobryttus gulosus*: Average Number of Parasites per Host.

	Apr.	May	July	Aug.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Number of hosts examined.....	7	4	5	6	12	10	10	10	10	10	5
<i>Ancyrocephalus</i> sp.....	0	0	0	0	0	0	0	0	0	11	6.4
<i>Paramphistomum stunkardi</i>	0	.4	0	1.5	.1	.3	.3	0	.4	.1	1
<i>Philometra</i> cysts.....	0	0	0	0	1.7	2.3	1.7	1.1	.2	.9	.6
<i>Spinitectus carolini</i>	1.3	.2	.4	6.3	.7	.6	1.3	1.6	.6	1.2	1.6
Strigeid cysts.....	4.2	5.5	8.4	19	4.3	4.7	3.8	4.4	4.2	2.1	.4
Average internal parasites per host....	5.5	6.1	8.8	29.8	6.7	7.9	7.3	8.2	5.4	4.3	3.6

TABLE VI. *Eupomotis gibbosus*: Percentage of Hosts Infested.

	Apr.	June	July	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Number of hosts examined.....	3	5	5	5	8	10	10	10	10	10	5
Percentage of hosts infested.....	100	100	100	100	100	100	100	100	100	100	100
<i>Ancyrocephalus</i> sp.....	0	0	0	0	0	0	0	0	0	30	40
<i>Paramphistomum stunkardi</i>	0	0	0	40	48	30	10	20	20	10	20
<i>Philometra</i> cysts.....	0	0	0	20	33	30	70	60	40	60	100
<i>Spinitectus carolini</i>	33	20	20	20	48	20	60	60	70	80	60
Strigeid cysts.....	100	100	100	100	100	100	100	100	100	100	100
Unidentified nematode cysts.....	0	0	0	0	0	0	30	60	40	0	0
<i>Diplostomum</i> cysts.....	67	60	40	40	50	0	0	20	20	10	0

TABLE VII. *Eupomotis gibbosus*: Average Number of Parasites per Host.

	Apr.	June	July	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Number of hosts examined.....	3	5	5	5	8	10	10	10	10	10	10
Average per host*.....	26.3	10.6	16.8	11.9	18.8	13.7	24.2	20.7	15.6	9.6	8.8
<i>Paramphistomum stunkardi</i>	0	0	0	1	4.7	.5	.6	.4	.3	.4	1.4
<i>Philometra</i> cysts.....	0	0	0	.6	2.5	.6	5.6	1.6	2.1	.9	2
<i>Spinitectus carolini</i>	1.6	.4	.2	1.8	1	.4	1.8	1	2.3	4	1.8
Strigeid cysts.....	24.7	10.2	16.6	8.5	10.6	12.2	12.5	12.9	9.7	4.3	3.6
Unidentified nematode cysts.....	0	0	0	0	0	0	3.7	4.8	1.2	0	0
<i>Diplostomum</i> cysts.....	9	33.3	1.4	3.8	6.5	0	0	3.3	.3	.1	0
<i>Ancyrocephalus</i> sp.....	0	0	0	0	0	0	0	0	0	.3	1.4

*Average for internal parasites - does not include dermal *Diplostomum* sp. cysts or *Ancyrocephalus* sp. from the gills.

TABLE VIII. *Enneacanthus gloriosus*: Percentage of Hosts Infested.

	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Number of hosts examined.....	4	3	9	6	5	10	10	10	10	10	10	9	10
Percentage of hosts infested.....	100	100	33	50	80	80	90	70	100	100	100	100	60
<i>Neoechinorhynchus</i>													
<i>cylindratus</i>	0	0	0	0	0	0	0	0	40	20	40	33	20
<i>Ancyrocephalus</i> sp.....	25	0	0	0	0	0	0	0	0	0	0	22	0
<i>Philometra</i> cysts.....	0	0	11	17	80	40	80	60	70	90	40	66	10
<i>Phyllodistomum pearsei</i>	0	0	0	60	0	0	0	10	10	0	20	11	0
Protocephalan cysts.....	0	0	0	0	0	0	0	0	90	80	60	66	10
Spiruroids.....	75	33	22	0	0	60	10	0	0	0	0	55	30
Unidentified larval nematodes.....	50	66	0	0	0	0	50	50	100	90	90	50	20

TABLE IX. *Enneachanthus gloriosus*: Average Number of Parasites per Host.

	pr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Number of hosts examined..	4	3	9	6	5	10	10	10	10	10	10	9	10
Average per host*.....	.1	1.7	1.5	4.8	2.6	4.8	11.9	4.9	12.3	11.6	8.2	8.2	2.2
<i>Neoechinorhynchus</i>													
<i>cylindratus</i>	0	0	0	0	0	0	0	0	1.2	.3	1.3	.8	.4
<i>Ancyrocephalus</i> sp.....	1.3	0	0	0	0	0	0	0	0	0	0	3	0
<i>Philometra</i> cysts.....	0	0	1.1	1.5	2.6	3.1	11.8	4.7	2.9	5.8	3	1.6	.2
<i>Phyllodistomum pearsei</i>	0	0	0	3.3	0	0	0	.1	.1	0	.2	.1	0
Protocephalan cysts.....	0	0	0	0	0	0	0	0	8.9	5.5	3.7	4.4	.4
Spiruoids.....	1	1.7	.4	0	0	1.2	.1	0	0	0	0	1.2	1.1

The unidentified larval nematodes ranged from about 20 to an estimate of 500 with a maximum average (estimated) in December of 300.

*Average without the larval nematodes and *Ancyrocephalus*.

TABLE X. *Ameiurus natalis*: Percentage of Hosts Infested.

	May	June	July	Aug.	Sept.	Oct.	Nov.
Number of hosts examined.	2	3	5	14	5	9	6
Percentage infested.....	100	33.3	100	71.4	100	88.8	83.3
<i>Philometra</i> cysts.....	50	0	60	57.1	80	77.7	83.3
<i>Phyllodistomum carolini</i>	0	0	0	0	0	11	33
<i>Plagiorchis ameiurensis</i>	100	0	40	28.6	60	44.4	33.3

TABLE XI. *Ameiurus natalis*: Average Number of Parasites per Host.

	May	June	July	Aug.	Sept.	Oct.	Nov.
Number of hosts examined.	2	3	5	14	5	9	6
Average per host.....	6	.7	3.5	6	2.6	15.2	55.8
<i>Philometra</i> cysts.....	10	0	2.8	5.3	2.4	12	51.3
<i>Phyllodistomum carolini</i>	0	0	0	0	0	1.1	3.2
<i>Plagiorchis ameiurensis</i>	2	0	.6	.7	.2	2.3	2.2

TABLE XII. *Triturus viridescens*: Comparison of the average infestation during the different stages in the life cycle.

	Aquatic	Transitional	Terrestrial
Number examined.....	32	5	6
<i>Acanthocephalus acutulus</i>	1.8	0	0
<i>Cappillaria</i> sp.....	2.3	.4	.3
<i>Cosmocerca dukae</i>4	0	0
<i>Opithodiscus americanus</i>	2.3	0	0
<i>Philometra</i> sp. cysts.....	1.7	.3	0
<i>Plagitura salamandra</i>	3.2	3.3	3.8
Total Infection.....	11.6	4.2	4.

TABLE XIII. Comparison of the Parasites of Two Centrarchids
Eupomotis gibbosus and *Chaenobryttus gulosus*.

	Number examined	<i>Ancyrocephalus</i> sp.	Diplostomum cysts	<i>Paramphistomum</i> <i>Stunkardi</i>	Philometra cysts	<i>Spinitectus</i> <i>carolinus</i>	Strigoid cysts	Leeches	Total
<i>Eupomotis gibbosus</i>									
Average.....	66	.2	.7	.5	1.7	1.7	11.5	.2	18.5
Percent.....		7.5	12.1	18.2	48.6	56	100	18.2	100
<i>Chaenobryttus gulosus</i>									
Average.....	77	1.8	0	.3	1.2	1.1	3.2	.1	8
Percent.....		17	0	22	38.8	44.2	80.5	10.4	88.3

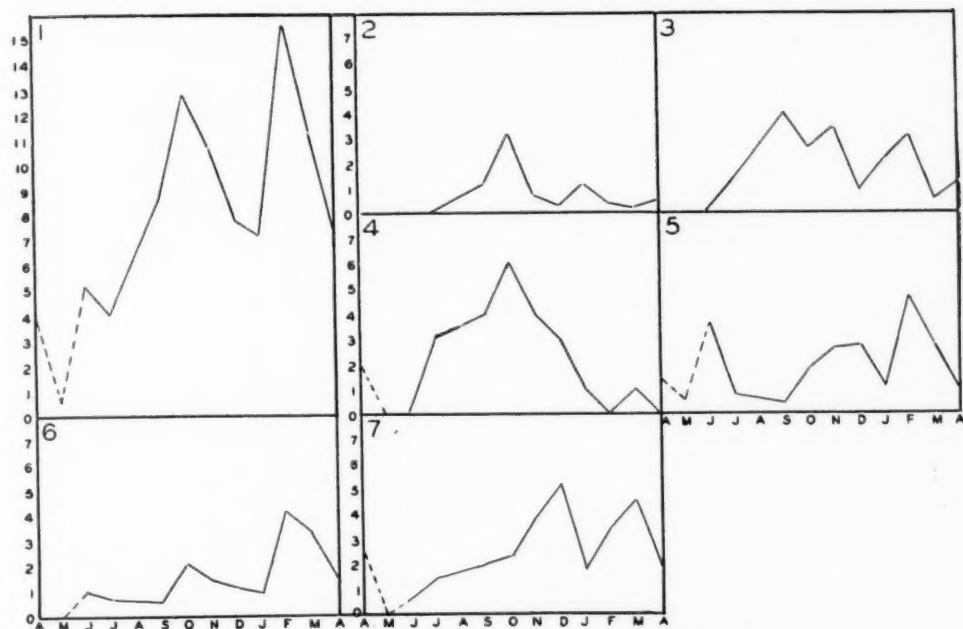


FIG. 1. Average number of parasites infesting *Triturus viridescens*. 1, total; 2, *Acanthocephalus aculeatus*; 3, *Capillaria* sp.; 4, *Cosmocerca dukae*; 5, *Opithodiscus americanus*; 6, *Philometra* cysts; 7, *Plagitura salamandra*.

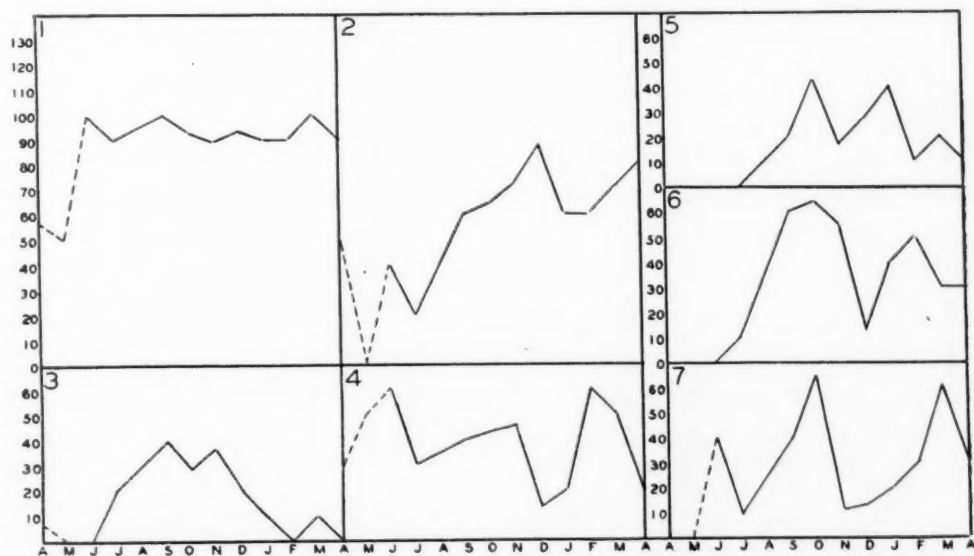


FIG. 2. Percentage of *Triturus viridescens* infested. 1, total; 2, *Plagitura salamandra*; 3, *Acanthocephalus aculeatus*; 4, *Capillaria* sp.; 5, *Cosmocerca dukae*; 6, *Opithodiscus americanus*; 7, *Philometra* cysts.

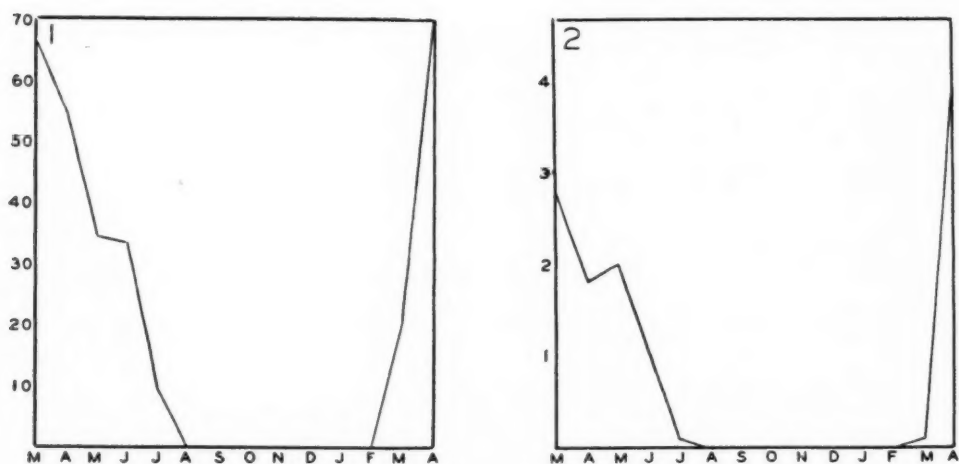


FIG. 3. *Acris gryllus*. 1, Percentage of hosts infested; 2, Average number of parasites per host.

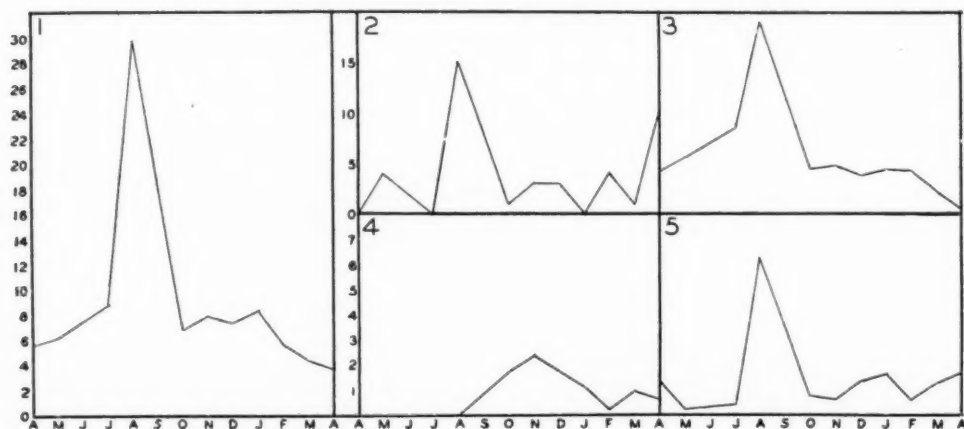


FIG. 4. Average number of parasites infesting *Chaenobryttus gulosus*. 1, total; 2, *Paramphistomum stunkardi*; 3, Strigeid cysts; 4, *Philometra* cysts; 5, *Spinitectus carolinus*.

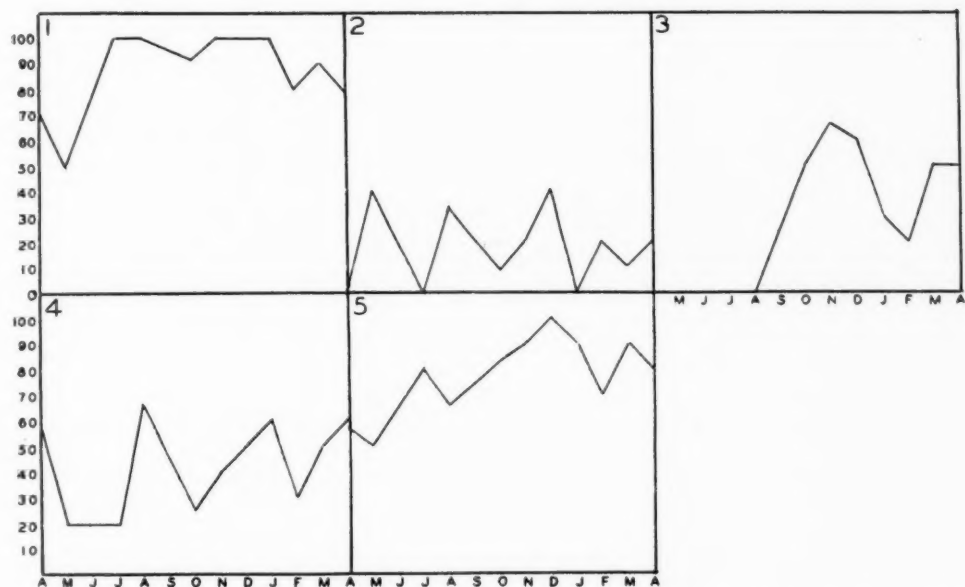


FIG. 5. Percentage of *Chaenobryttus gulosus* infested. 1, total; 2, *Paramphistomum stunkardi*; 3, *Philometra* cysts; 4, *Spinitectus carolinus*; 5, Strigeid cysts.

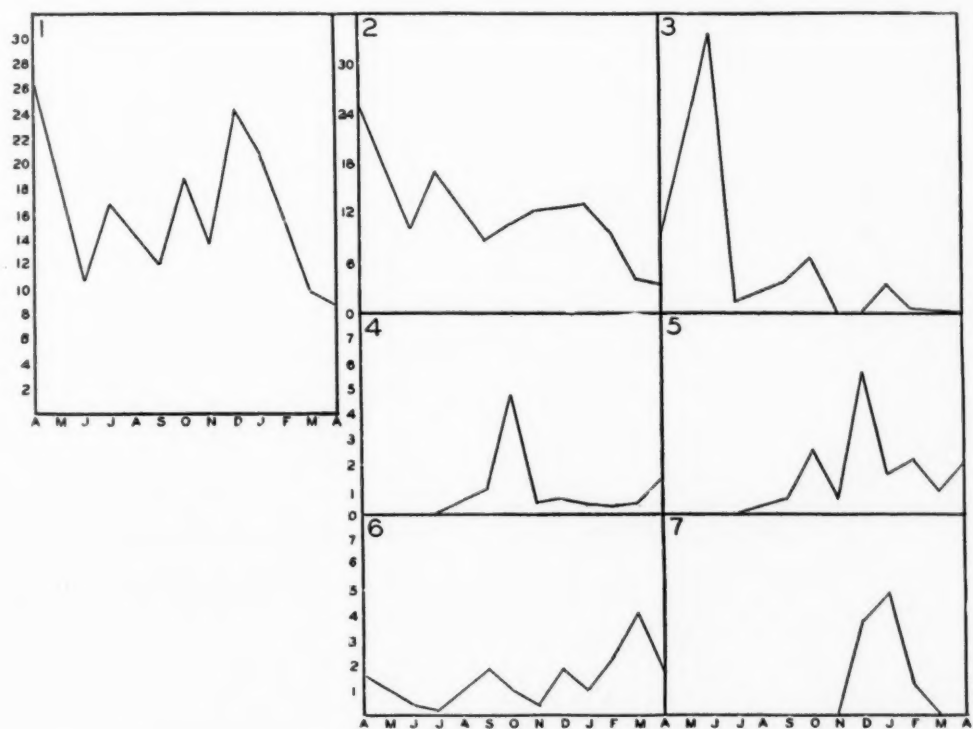


FIG. 6. Average number of parasites infesting *Eupomotis gibbosus*. 1, total; 2, Strigeid cysts; 3, *Diplostomum* cysts; 4, *Paramphistomum stunkardi*; 5, *Philometra* cysts; 6, *Spinitectus carolinus*; 7, Unidentified nematode cysts.

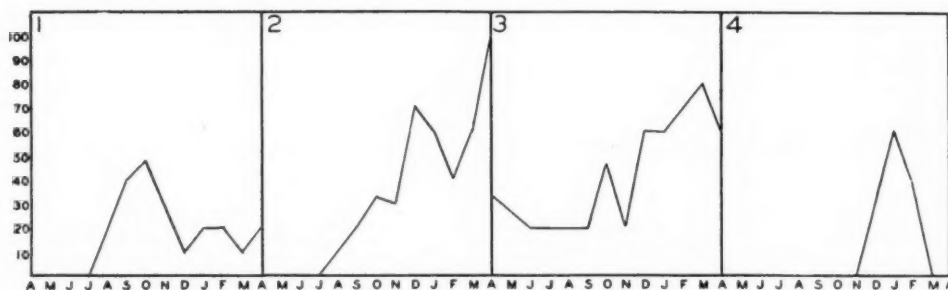


FIG. 7. Percentage of *Eupomotis gibbosus* infested. 1, *Paramphistomum stunkardi*; 2, *Philometra* cysts; 3, *Spiniectus carolinus*; 4, Unidentified nematode cysts.

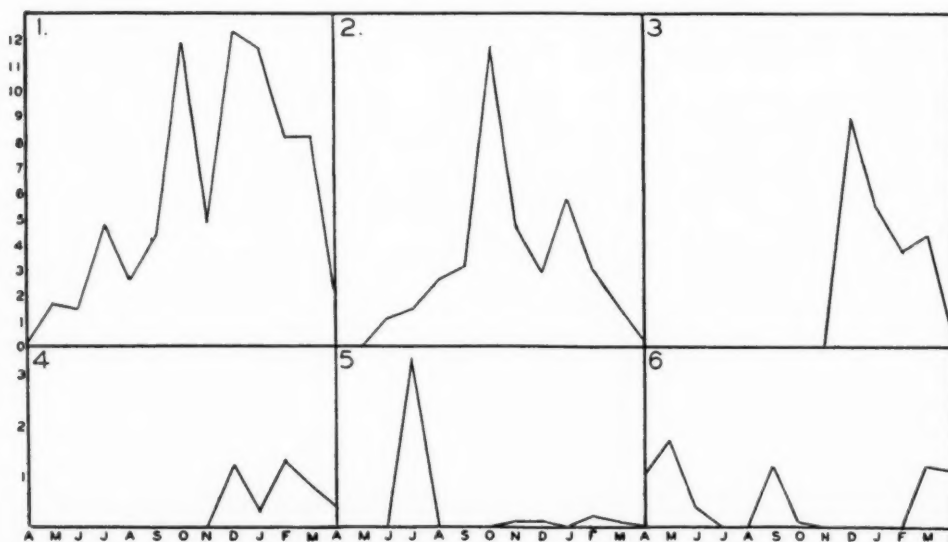


FIG. 8. Average number of parasites infesting *Ennecochanthus gloriosus*. 1, total; 2, *Philometra* cysts; 3, *Protocephalan* cysts; 4, *Neoechinorhynchus cylindratus*; 5, *Phyllodistomum pearsei*; 6, Spiruroid worms.

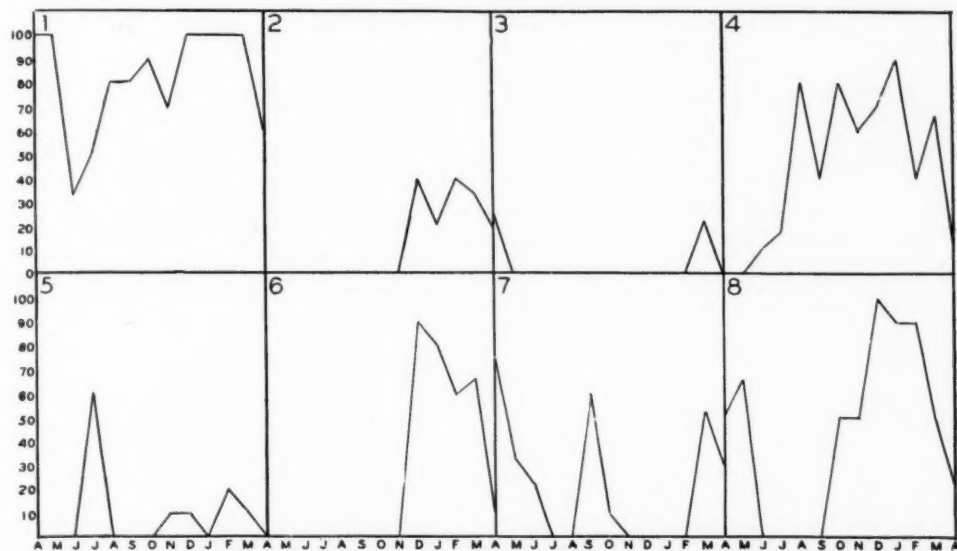


FIG. 9. Percentage of *Enneachanthus gloriosus* infested. 1, total; 2, *Neoechinorhynchus cylindratus*; 3, *Ancyrocephalus* sp.; 4, *Philometra* cysts; 5, *Phyllodistomum pearsei*; 6, *Protocephalan* cysts; 7, *Spiruroid* worms; 8, larval nematodes.

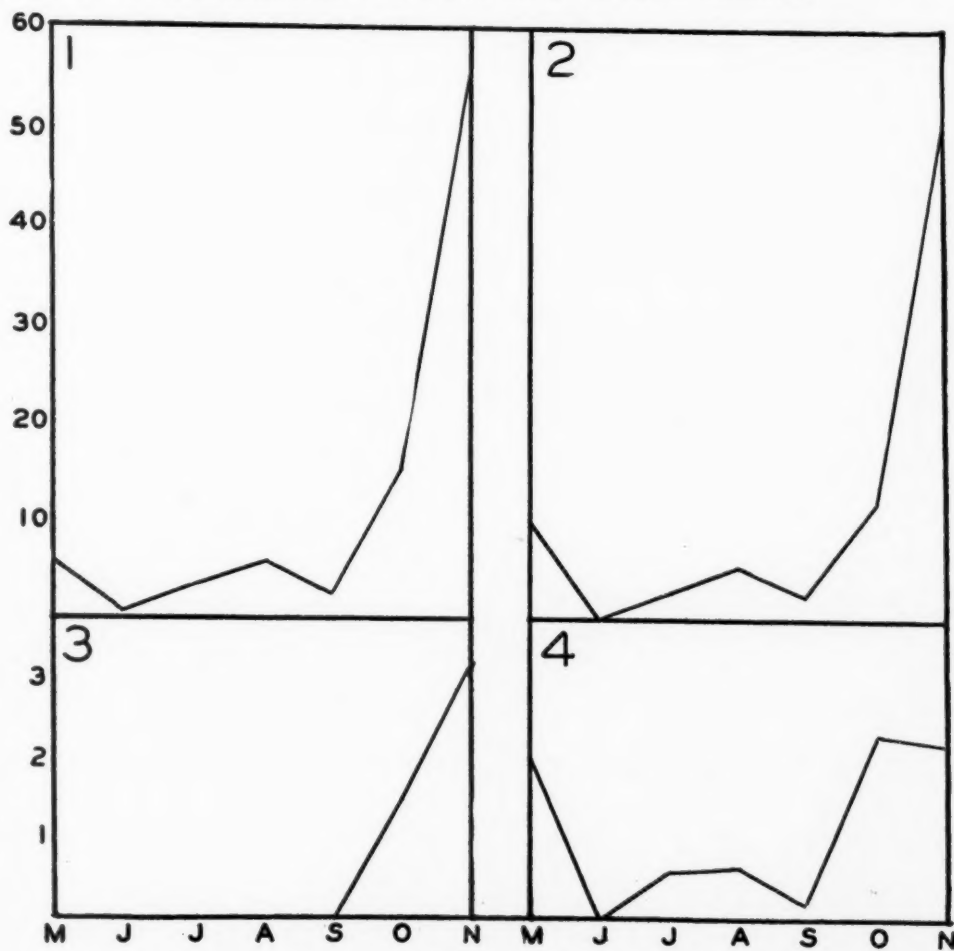


FIG. 10. Average number of parasites infesting *Ameiurus natalis*. 1, total; 2, *Philometra* sp. cysts; 3, *Phyllodistomum carolini*; 4, *Plagiorchis ameiurensis*.